

THE PRESENCE OF *MICROPTERUS SALMOIDES* (LARGEMOUTH BASS)
INFLUENCES THE POPULATIONS OF *RANA DRAYTONII* (CALIFORNIA RED-
LEGGED FROG) AND *PSEUDACRIS REGILLA* (PACIFIC TREEFROG) IN TWO
PONDS IN SANTA BARBARA COUNTY, CALIFORNIA

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TITLE: The Presence of *Micropterus salmoides* (largemouth bass) Influences the Populations of *Rana draytonii* (California red-legged frog) and *Pseudacris regilla* (Pacific treefrog) in Two Ponds in Santa Barbara County, California

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ABSTRACT

The Presence of *Micropterus salmoides* (Largemouth Bass) Influences the Populations of *Rana draytonii* (California Red-legged Frog) and *Pseudacris regilla* (Pacific Treefrog) in Two Ponds in Santa Barbara County, California

Kenneth Lee Gilliland

Alien fish have been implicated in the decline of *Rana draytonii* (California red-legged frog) and *Pseudacris regilla* (Pacific treefrog) populations. *Micropterus salmoides* (largemouth bass) is a common sport fish that has been introduced into the sympatric range of these two anuran species; however, no studies have investigated the individual influence that this alien fish has on these two species. I conducted *M. salmoides* control or eradication experiments during a four year study in two ponds within the Transverse Mountain Range of Santa Barbara County, California. Changes in the densities of all life stages of *R. draytonii* and *P. regilla* were assessed through repeated visual encounter surveys. In response to the manipulations of the *M. salmoides* populations there was an increase in the density of both species. For *R. draytonii*, this salient increase in density was recorded in the larval and metamorph life stages. For *P. regilla*, a slight, yet steady increase in the density of adult, metamorph, and larval life stages was recorded. My results suggest that *M. salmoides* can be controlled or eradicated from lentic waterbodies and provides reasonable evidence that the negative effects of this species on *R. draytonii* and *P. regilla* populations can be minimized or reversed. The reversal of these effects may translate into increases in the densities and potential recruitment of these two native anurans. Therefore, my results provide tentative support that the control or eradication of *M. salmoides* where they cohabitate with these two species may be a viable conservation measure for *R. draytonii* and *P. regilla* populations. Since my study was performed at a very local scale and all results are strictly observational and descriptive, additional studies should be performed at a larger spatial scale and buttressed with controlled laboratory and field enclosures experiments to identify the causal factors responsible for the identified patterns.

Keywords: *Rana draytonii*, California red-legged frog, *Pseudacris regilla*, Pacific treefrog, *Micropterus salmoides*, largemouth bass, alien fish, anuran declines

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INTRODUCTION

In California and much of western North America, amphibian population declines are occurring, and several causal factors have been proposed including disease (Kiesecker and Blaustein 1997; Kiesecker et al., 2001; Blaustein et al., 2005; Fellers et al., 2007), increased use of pesticides and air pollution (Davidson et al., 2001; Relyea and Mills 2001; Kiesecker 2002), habitat destruction (Davidson et al., 2002), over-exploitation (Jensen and Camp 2003; Jennings and Hayes 1985), climate change (Pounds et al., 1999), UV-B radiation (Blaustein et al., 1997; Anzalone et al., 1998; Blaustein et al., 1998), and alien predators and competitors (Kupferburg 1997; Knapp and Matthews 2000; Vredenburg 2004; Pope 2008). Recent studies have suggested that amphibian declines are potentially influenced by a number of context-specific interactions of multiple stressors and synergisms between these causal factors (Blaustein and Kiesecker 2002; Kiesecker 2002; Pounds et al., 2006).

Our limited ability to ameliorate factors including climate change and disease that affect amphibian populations over time scales relevant to contemporary conservation actions make addressing these factors difficult (Knapp et al., 2007). Nevertheless, some declines caused by alien species may be reversed relatively quickly (Pope 2008; Knapp et al., 2007; Mullin 2004; Vredenburg 2004). In California, reversal of the negative effects of alien species on amphibians has been suggested by a number of studies showing that the removal or disappearance of the

alien species results in the recovery of local amphibian populations (Pope et al., 2008; Knapp et al., 2001; Knapp 2005; Vredenburg 2004). Therefore, the restoration of amphibian habitats to their historic alien-free condition could be a relatively simple way to recovery for some native amphibians.

Fish are the most widespread alien species implicated in amphibian declines (Stebbins and Cohen 1995). Alien fish alter the local distribution and abundance of amphibian communities through reductions or extirpations of their populations (Petranka 1983; Hecknar and M'Closkey 1997; Knapp et al., 2001; Pilliod and Peterson 2001). Amphibians with complex life histories including aquatic egg and larval life stages are particularly vulnerable to the influences of these alien predators (Kats and Ferrer 2003). Many native amphibian species lack an evolutionary history with fish, and therefore lack evolutionary adaptations to compensate for the influences of alien fish introduced into their range (Diamond and Case 1986; Kats and Ferrer 2003). The impact of alien fish is usually strongest upon amphibian species that evolved without fish (Kats and Ferrer 2003). The magnitude of the alien fish impact is often correlated to the alien's taxonomic distinctiveness within the recipient community (Ricciardi and Atkinson 2004), and much of the variation in an alien's impact across different amphibian communities can be explained by the community's prior experience with native species that occupy similar niches (Diamond and Case 1986).

In California, the influences of individual species of alien fish on native amphibians are often obscured because many of these habitats contain multiple

alien species (Fisher and Shaffer 1996; Alvarez et al., 2003; Kiesecker and Blaustein 1998). The influences of individual species are often confounded because there may be synergisms between the alien species present that magnify the relative impact on the native amphibians (Kiesecker and Blaustein 1997; Kiesecker and Blaustein 1998).

Alien fish are spread through intentional and accidental human-mediated introductions. Intentional human-mediated introductions are usually intended to provide game for sport anglers or to be used as biocontrol agents. Accidental introductions include instances when alien fish that have been stocked as game or biological control agents are dispersed to unintended areas (Bradford 1989; Kolar and Lodge 2000). These fish are often accidentally introduced to unanticipated areas during flood events (Bradford 1989).

Salmonids and centrarchids have been intentionally introduced to numerous water bodies throughout California to establish recreational fisheries. They have also been accidentally introduced to unintended areas of these watersheds (Bradford et al., 1993; Moyle 2002; Bradford 1989). These human-mediated introductions of alien sport fish are often successful in creating recreational opportunities, but they can have unintended consequences to native amphibians (Pope et al., 2008; Knapp et al., 2001; Knapp 2005; Vredenburg 2004). The use of *Gambusia* sp. (mosquitofish) as a biocontrol agent of mosquitoes and other pests has motivated their intentional introduction throughout California. Although intentionally and accidentally established *Gambusia* sp. populations prey upon mosquitoes (Miura et

al., 1979; Bence, 1988), they also consume larval amphibians (Webb and Joss 1997; Goodsell and Kats 1999).

Evidence in support of the widely accepted hypothesis that alien fish contribute to amphibian, and specifically anuran declines in California, has accumulated through a combination of correlational and experimental investigations. Correlational studies performed at local, watershed, and landscape scales have indicated a negative relationship between the presence of alien fish and the extirpation and reduction of anuran populations (Bradford 1989; Bradford et al., 1993; Knapp and Matthews 2001; Pilliod and Peterson 2001). Although correlative studies report on the ultimate outcome of the interaction between alien fish and native anurans at broad scales, they do not provide the proximate mechanisms responsible for the anuran declines.

Experimental studies buttress support for correlational evidence by investigating the proximate mechanisms responsible for the presence of alien fish and the extirpation or reduction of anuran populations. Under laboratory and simplified field conditions, experimental studies place alien fish together with native anurans. These studies have shown that when raised in the presence of alien fish, anurans experience reductions in fitness (depressed growth, smaller size at metamorphosis) (Kiesecker and Blaustein 1997) or are eliminated due to high mortality (Kiesecker and Blaustein 1998; Lawler et al., 1999; Vredenburg 2004). Experimental studies are not usually considered controversial, but concerns have been expressed that experimental laboratory or some field settings are overly

simplistic (Lawler et al., 1999). Contemporary experimental studies have attempted to challenge this criticism by investigating the response of native amphibians to the experimental eradication of alien fish under field conditions at broader spatial scales (Pope et al., 2008; Knapp and Matthews 1998; Knapp et al., 1996; Vredenburg 2004).

The majority of correlational and experimental studies on the ecology of alien fish and native anurans in California have focused on lentic environments within protected areas of the Sierra Nevada Mountain Range within the historic range of *Rana muscosa* (mountain yellow-legged frog). Conducting these studies within designated protected areas was beneficial since land management objectives and activities remain relatively constant and these areas are relatively free of many other anthropogenic influences that have been identified to negatively affect biodiversity.

Rana muscosa has been extirpated from at least 50% of its historic range (Bradford et al., 1994; Drost and Fellers 1996; Jennings 1996) and causal factors including UV-B radiation (Blaustein et al., 1994; Anzalone et al., 1998) and environmental pollutants transported from agricultural in the Central Valley (Cory et al., 1970; Zabik and Sieber 1993; Datta et al., 1998; Davidson and Knapp 2007) may have also played a role in their decline. However, correlational evidence collected at the local scale suggested that predation by alien trout may have contributed to this range-wide decline (Bradford 1989; Bradford et al., 1993). To examine if the lack of overlap between alien trout and *R. muscosa* was a local or

landscape phenomenon, Knapp and Matthews (2000) investigated the distribution of *R. muscosa* and alien trout within protected areas at a much larger scale (100,000 ha). Their results indicated that the presence of alien trout was negatively correlated with the presence of *R. muscosa* at the scale of landscape, individual watersheds, and individual water body. This negative correlation also indicated that this lack of overlap may be a result of similar habitat requirements (deep water bodies) between the taxa (Knapp and Matthews 2000).

The experimental eradication of alien trout has also been shown to significantly increase *R. muscosa* populations within a watershed. Vredenburg (2004) utilized gill nets to eradicate populations of alien trout (*Oncorhynchus* sp., *Salmo* sp., and *Salvelinus* sp.) in five lakes of the Sierra Nevada Mountain Range. *Rana muscosa* numbers in lakes before trout removal (pretreatment conditions) were not statistically different from control lakes that contained trout. Following the removal of trout, *R. muscosa* populations in the treatment lakes increased significantly when compared to lakes that contained trout. Investigations into the proximate mechanisms responsible for the observed increases in *R. muscosa* populations using field enclosures indicated that trout readily prey upon newly hatched *R. muscosa* larvae and larvae from past reproductive seasons.

Knapp et al., (2007) used a similar experimental methodology to examine if the results from Vredenburg (2004) were local or generalizable to other parts of the contemporary distribution of *R. muscosa*. Additional support of Vredenburg's (2004) study were important since potential amphibian stressors (e.g., climate

change, disease, pesticides) are unlikely to be evenly distributed across a species' range (Davidson 2004; Fisher and Schaffer 1996; Knapp et al., 2007), and the *R. muscosa* population studied by Vredenburg et al. (2004) was genetically divergent from those studied by Knapp et al. (2007) (Vredenburg et al., 2007). Alien trout were eradicated from six lakes far from the Vredenburg study site, and significantly more *R. muscosa* were observed one year after alien fish eradication. *Rana muscosa* densities in trout-free control lakes were significantly lower than lakes where trout were recently eradicated. Recovery of *R. muscosa* populations in the experimental lakes was due to a combination of the successful reproduction of resident and emigrating adults, successful metamorphosis of their progeny, and emigration of subadult frogs to previously unoccupied habitats from adjacent trout-free habitats.

Although substantial evidence supports alien fish as causing *R. muscosa* population declines, *R. muscosa* have been extirpated from historically trout-free lakes and watersheds indicating that other factors may have played a role in the decline of the species. Davidson and Knapp (2007) investigated the relative importance of alien fish and airborne agricultural contaminants (i.e., pesticides and herbicides) to the current distribution of *R. muscosa*. They found that both alien fish and agricultural contaminants may be contributing to *R. muscosa* declines, and that agricultural contaminants may be having a greater overall negative effect on the current distribution of *R. muscosa*. The negative effect of agricultural contaminants may be a result of pesticide-induced immunosuppression (Taylor et al., 1999;

Kiesecker 2002; Gilbertson et al., 2003), which may result in an increase of the susceptibility of *R. muscosa* to disease including chytridiomycosis (*Batrachochytrium dendrobatidis*). Support for pesticide-induced immunosuppression comes from unsuccessful translocations of *R. muscosa* into areas with high upwind pesticide use (Davidson and Knapp 2007; Fellers et al., 2004) and the presence of high pesticide concentrations in the tissues of translocated *R. muscosa* (Fellers et al., 2007). These translocations were conducted prior to the identification of chytridiomycosis in amphibians (Berger et al., 1998), but die-offs of the translocated anurans were consistent with chytridiomycosis infection (Fellers et al., 2007). More recently, chytridiomycosis has been demonstrated as a proximate cause of numerous *R. muscosa* population declines (Rachowicz et al., 2006). Lastly, factors like climate change that have yet to be realized may also have the potential to exacerbate the factors responsible for these population declines (Lacan et al., 2008).

Although the influences of individual, multiple, and synergistic stressors responsible for *R. muscosa* declines remain enigmatic, correlational and experimental support of the influences of alien fish on *R. muscosa* populations provide a framework for further investigations into the influences of alien fish on native California anurans. *Rana draytonii* (California red-legged frog) and *Pseudacris regilla* (Pacific treefrog) are two sympatric, California native anurans (Stebbins 2003) that may also have declined due to alien fish (Hayes and Jennings 1986; Fisher and Schaffer 1996; USFWS 1996; Matthews et al., 2004). Since alien

fish may influence the population dynamics of these two California native species, I investigated how the control and eradication of one alien fish species, *Micropterus salmoides* (largemouth bass), affects these two species.

Although centrarchids have been suggested as a causal factor in the decline of *R. draytonii* (Hayes and Jennings 1986; Fisher and Schaffer 1996; USFWS 1996), but not *P. regilla* (due to a dearth of scientific investigations), to the best of my knowledge, there have been no studies performed on the individual influence that *M. salmoides* has on these anurans. Fortunately, I was able to investigate the individual interaction between *M. salmoides*, *R. draytonii*, and *P. regilla* at my study area in Santa Barbara County, because it only contained this single alien fish species. Given that *M. salmoides* are contemporaneously used to establish recreational fisheries within the sympatric range of *R. draytonii* and *P. regilla*, investigations into the influences of this alien fish species on native anurans may be important for land management decisions.

Currently, *R. draytonii* have been extirpated from approximately 70 percent of their historical distribution (Jennings 1988; Jennings and Hayes 1994). Some researchers have suggested that alien predatory species are the major factor responsible for this range reduction (Hayes and Jennings 1986; Fisher and Shaffer 1996; USFWS 1996; USFWS 2002). Strong negative correlations between the presence of alien fish, *R. catesbeiana* (American bullfrog), and *R. draytonii* have been identified (Jennings and Hayes 1986; Fisher and Shaffer 1996), yet these data are confounded by the presence of a variety of land management activities and the

presence of multiple alien species (Jennings and Hayes 1986; Knapp 1996; Kiesecker and Blaustein 1998; Adams et al., 2003; Alvarez et al., 2003).

Although the influences of *M. salmoides* on *R. draytonii* population dynamics remain obscure, Kiesecker and Blaustein (1998) used field enclosures to investigate the effects of alien *R. catesbeiana* and *M. dolomieu* (smallmouth bass) on the microhabitat use, growth, and survival of larval *R. aurora* (northern red-legged frog). *Micropterus dolomieu* are efficient anuran larval predators (Scott and Crossman 1973; Kruse and Francis 1977; Kiesecker and Blaustein 1998), but their presence alone had little affect on *R. aurora*. In contrast, the combined presence of *M. dolomieu* and *R. catesbeiana* decreased the postmetamorphic biomass, increased the larval developmental time, and decreased the survival of *R. aurora*. The synergistic influence of *M. dolomieu* and *R. catesbeiana* likely led to increased *M. dolomieu* depredation of *R. aurora*. In the presence of *R. catesbeiana*, larval *R. aurora* had a microhabitat shift to deeper water. This microhabitat shift likely led to increased overlap between larval *R. aurora* and *M. dolomieu*, increasing the potential for *R. aurora* depredations. Although *M. dolomieu* and *M. salmoides* are congeners, water depth selection by these two species is different. *M. salmoides* are predominately found at a water depth of 0.1 to 3 m (Moyle 2002), and *M. dolomieu* are usually occur at depths over 1.5 m (Kiesecker and Blaustein 1998). Therefore, the water depth preferences of *M. salmoides* may exacerbate the influences on larval *R. draytonii* and *P. regilla* since they often occur in similar microhabitats.

Additional experimental evidence comes from Alvarez et al., (2003) who performed an alien fish removal experiment in seven lentic environments containing *R. draytonii* in Contra Costa County, California. The ponds supported alien fish populations with variable compositions including combinations of *Ameiurus nebulosus* (brown bullhead), *A. catus* (white catfish), *Ictalurus punctatus* (channel catfish), *Lepomis macrochirus* (bluegill), *Gambusia affinis* (western mosquitofish), and *M. salmoides*. Following eradication of these alien fish, the abundance of all life stages of *R. draytonii* increased. The number of metamorphic *R. draytonii* had the most dramatic increase. For example, in a single pond when alien fish were present the highest number of *R. draytonii* metamorphs observed was 15, but 650 metamorphs were observed following alien fish eradication. These results indicate that alien fish removal caused a marked increase in larval and metamorph survivorship which likely caused increases in recruitment of metamorphs into the adult reproductive population. Unfortunately, this study was unable to document the individual effects of each alien species (Jennings and Hayes 1985; Knapp 1996; Kiesecker and Blaustein 1998; Adams et al., 2003).

In western North America, *P. regilla* is the most abundant amphibian (Brattstrom and Warren 1955). Due to the ubiquitous nature of this species it has been difficult to determine if *P. regilla* populations are declining (Fisher and Schaffer 1996; Drost and Fellers 1996). Detecting declines in this species are difficult because its populations fluctuate naturally and there is a lack of long-term studies on its population dynamics. Compared to *R. draytonii*, *P. regilla* may be

less susceptible to alien fish, because *P. regilla* are more plastic in their breeding habitat requirements, adults are predominately terrestrial, and larvae develop more quickly (Stebbins 2003; Schaub and Larsen 1978; Knapp 1996).

Matthews et al. (2004) showed that in the Sierra Nevada Mountain Range, alien trout negatively influence the distribution and abundance of *P. regilla*. Their results suggest that *P. regilla* has declined at the landscape scale where high levels of trout stocking occur. Likewise, Goodsell and Kats (1997) suggested that *G. affinis* may negatively affect stream-breeding *P. regilla*. Their laboratory predation trials indicated that in the presence of high densities of alternative prey (mosquito larvae), *G. affinis* still prey upon larval *P. regilla*. Furthermore, field predation trials indicated that 65 percent of the gut contents of *G. affinis* from streams in the Santa Monica Mountains of California contained *P. regilla* larvae.

Adams (2000) used field enclosure experiments to investigate the relative effects of pond permanence and the presence of *Lepomis gibbosus* (pumpkinseed), *L. macrochirus*, and *Perca flavescens* (yellow perch) and *R. catesbeiana* on larval *R. aurora* and *P. regilla*. Larval survival of both anurans was reduced to nearly zero in enclosures with these centarchids. Likewise, larval survival of both anurans was generally lower in permanent ponds containing alien species than in more ephemeral ponds free of aliens. Besides direct depredations, the presence of alien species in permanent ponds may have caused a reduction in foraging activity resulting in slower growth rates and increased predation rates by native aquatic

invertebrates or the alien species caused a trophic cascade reducing larval food availability (Adams 2000).

The presence of two California native anurans at my study site with different natural histories and potentially different interactions with *M. salmoides* provided the opportunity to investigate how this single alien fish species influences their local population dynamics. Over four years of study (2006 to 2009), I experimentally manipulated two *M. salmoides* populations through the application of two different fish control techniques in two ponds in the Transverse Mountain Range of Santa Barbara County. I performed *M. salmoides* control or eradication with a combination of water removal (Alvarez et al., 2003) and utilization of heavy equipment or gill netting (Pope 2007; Vredenburg 2004, Knapp et al., 2007; Knapp and Matthews 1998).

My initial goal was to investigate if the densities of the different life stages (larval, metamorph, and adult) of the anuran species changed following the manipulation of the *M. salmoides* populations. My second goal was to investigate if there was any correlation between the densities of the different life stages of *R. draytonii* and *P. regilla* at one pond before the application of *M. salmoides* control efforts, following the application of the two *M. salmoides* control techniques in this pond, and at a pond where *M. salmoides* eradication was achieved. I assessed changes in the densities of different life stages of *R. draytonii* and *P. regilla* populations with visual encounter surveys in both ponds.

FOCAL SPECIES

Rana draytonii (California red-legged frog)

At one time, *R. draytonii* (Baird and Girard 1852; Schaffer et al., 2004) was considered a subspecies of *R. aurora* (*Rana aurora draytonii*), but genetic evidence (mtDNA) revealed that *R. draytonii* is a diagnosably distinct species with a narrow range of overlap with *R. aurora* in Mendocino County, California (Schaffer et al., 2004).

Rana draytonii is endemic to California and Baja California (Lindsale 1932; Jennings and Hayes 1994; Schaffer et al., 2004) and is the largest native frog within this range. Historically, this species occupied numerous foothill and coastal watersheds west of the Sierra-Cascade Mountains at elevations below 1500 m (Jennings and Hayes 1986; USFWS 1996). The eastern range limit of this species was Shasta County to Tulare County and spanned the Great Central Valley from Mendocino County south to Baja California (Fellers 2005). By the early 1990s, this species had been extirpated from approximately 70 percent of its historical range (Jennings 1988; Jennings and Hayes 1994), causing the U.S. Fish and Wildlife Service (USFWS) to list *R. draytonii* as a federally threatened species in 1996 (USFWS 1996), and the California Department of Fish and Game (CDFG) to designate this species as a Species of Special Concern (Jennings and Hayes 1994).

Rana draytonii leads a highly aquatic lifestyle and is commonly found in or near water. Breeding habitat for this species includes perennial and intermittent

ponds, streams, marshes, and lagoons. Non-breeding habitats includes any area within 2 to 3 km of breeding sites that has sufficient vegetative or surface object cover that remains cool and moist (Fellers 2005; Bugler et al., 2003; Fellers and Kleeman 2007; Tatarian 2008; Rathbun et al., 1997). Some adult *R. draytonii* remain at the breeding site year-round, while others usually move into upland habitats within 0.5 km from the breeding site, but have been observed to move up to 3 km from the breeding site (Rathbun et al., 1997; Fellers 2005; Fellers and Kleeman 2007).

Males in this species mature in two years and females mature in three years (Jennings and Hayes 1985). They usually breed in late December through March, with most egg deposition taking place in Santa Barbara County in January and February (personal observation). This species has a moderate clutch size of 300 to 4,000 eggs, with an average clutch size of 2,000 eggs (Fellers 2005; Storer 1925). Although over-wintering of larvae has been observed in this species (Fellers et al., 2004), metamorphosis is typically completed in 3.5 to 7 months with metamorph emergence occurring from May to September (Storer 1925; Wright and Wright 1995; Jennings and Hayes 1989).

Threats to this species include overexploitation that occurred in the late-1800s (Jennings and Hayes 1985), habitat loss and fragmentation (Jennings 1988), the introduction of *R. catesbeiana* (Moyle 1973; Hayes and Jennings 1986), forestry activities (USFWS 1996; USFWS 2002), alien predatory fish (Hayes and Jennings 1986; Fisher and Shaffer 1996; USFWS 1996; USFWS 2002) and potentially

chytridiomycosis (Padgett-Flohr 2008). Chytridiomycosis has been detected via a DNA-based polymerase chain reaction (PCR) assay (Boyle et al., 2004; Hyatt et al., 2007) in the adult *R. draytonii* population at the study ponds (R. Smith personal communication), but it remains unknown what influences chytridiomycosis has on the local and regional populations of the species (Padgett-Flohr 2008).

Pseudacris regilla (Pacific treefrog)

Pseudacris regilla (Baird and Girard 1852) is the most abundant amphibian in western North America (Brattstrom and Warren 1955) and in California (Wright and Wright 1995). *Pseudacris regilla* is endemic from Baja California to southeastern Alaska with its eastern range limits of this species range in western portions of Montana, Idaho, Utah, and Arizona (Rorabaugh and Lannoo 2005). In California, *P. regilla* occur from below sea level to an altitude of 3500 m (Brattstrom and Warren 1955; Bezy and Goldberg 1997). The contemporary distribution of *P. regilla* in California is similar to their historical range and their range-wide population does not appear to be in decline (Fisher and Schaffer 1996), yet some local population declines in the Sierra Nevada Mountain Range have been documented (Bradford et al., 1994; Matthews et al., 2001). *Pseudacris regilla* have no protected status throughout their contemporary range.

In southern California, *P. regilla* breed from November through July (Brattstrom and Warren 1955; Perrill 1984; Hollingsworth and Roberts 2001). Adult *P. regilla* are extremely plastic in their breeding habitat requirements and

have been observed breeding in permanent and ephemeral lakes, ponds, slow-moving streams, backwaters of large rivers, wet meadows, emergent marshes, forested swamps, reservoirs, muskegs, supratidal pools, golf course ponds, and irrigation ditches (Brattstrom and Warren 1955; Wright and Wright 1995; Stebbins 2003; Leonard et al., 1993; Gardner 1995; Roarabaugh et al., 2004). Adults usually leave their aestivation or over-wintering sites and move to breeding sites in winter and spring and leave the breeding site by early fall (Rorabaugh and Lannoo 2005). Following breeding, adults leave the breeding area and seek refuge on low shrubbery or cool, moist retreats used for aestivation and over-wintering; however, a few individuals may stay at the breeding area for relatively longer periods (Weitzel and Panik 1993). Throughout the breeding season, males may remain at one breeding area, or may move at least 400 m to other suitable breeding habitats (Schaub and Larsen 1978).

Throughout the breeding season, females lay 400 to 700 eggs (Stebbins 2003). In California, the mean clutch size is 267.7 eggs, and females may lay three or more clutches per season (Perrill and Daniel 1983). Larvae are usually found in quiet or slow-moving portions of their aquatic habitats with suitable abundances of algae, bacteria, diatoms, and organic and inorganic debris (Wassersug 1975; Wagner 1986). Depending on altitude and latitude, metamorphosis occurs between June and October (Leonard et al., 1997). Shortly after metamorphosis, metamorphs move out of the natal waters and seek refuge amongst low-lying shrubs or cool, moist retreats during mid-summer to early-fall (Schaub and Larsen 1978). Sexual

maturity for both sexes in this species is believed to occur within one year (Weitzel and Panik 1993).

As with *R. draytonii* at my study ponds, chytridiomycosis has been detected via a DNA-based PCR assay (Boyle et al., 2004; Hyatt et al., 2007) in the adult *P. regilla* population at the study ponds (R. Smith personal communication). Experimental exposure of chytridiomycosis fungus had no discernable affect on *P. regilla* larvae and metamorphs under laboratory conditions (Blaustein et al., 2005; Garcia et al., 2006), so it remains unknown what affect chytridiomycosis has on the local and regional populations of the species.

Micropterus salmoides (largemouth bass)

Micropterus salmoides (Lacepède 1802) is native to northeastern Mexico, much of the Mississippi River watershed, and north into southern Ontario and Quebec, Canada (Lee et al., 1980; Jenkins and Burkhead 1994). These popular game fish have been introduced to over 50 countries (Welcomme 1992), including the entire continental United States (Moyle 2002). *Micropterus salmoides* were originally introduced in California in 1891 (Dill and Cordone 1997).

This species is commonly found in farm ponds, lakes, reservoirs, sloughs, and river backwaters. *Micropterus salmoides* require warm shallow waters (<6 m) with moderate clarity and aquatic vegetation (Moyle 2002), and are often found in association with other alien fish. This species is highly tolerant of adverse water

quality conditions and has been observed to persist in waters approaching 36 to 37°C with 1 mg/L dissolved oxygen concentrations (Coutant 1975; Smale and Rabeni 1995).

Adult *M. salmoides* are gape-limited, solitary predators, often found in water between 0.1 to 3.0 m in depth (Moyle 2002). Individuals may stay in a single area with aquatic vegetation or submerged structures or may forage widely throughout their habitat. Behaviorally, *M. salmoides* foraging strategies are flexible and can consist of ambush, pursuit, or both. Furthermore, this species can change its foraging strategy based on the availability of prey, habitat type, experience, and body size (Schindler et al., 1997). Once *M. salmoides* exceed 10.0 to 12.5 cm in length they usually prey upon fish; however, adults occasionally prefer crayfish or all amphibian life stages (Lewis et al., 1961).

Micropterus salmoides females first spawn at 20.0 to 25.0 cm, usually during their second or third year (Moyle 2002). In southern California, *M. salmoides* usually spawn from March through June (Weaver and Ziebell 1976; Emig 1966; Miller and Kramer 1971). Each female spawns in multiple nests per season, which consist of 2,000 to 94,000 eggs or more depending on the size of the female. Males vigorously defend nest sites, eggs, and recently hatched fry (Moyle 2002). Following dispersal, fry, fingerlings, and juveniles forage and school close to shore near aquatic vegetation or submerged objects.

Micropterus salmoides have many of the general requirements necessary for successful invasion (Meffe and Carroll 1997; Holoway and Suarez 1999): they are

habitat generalists (Welcomme 1992), have broad dietary requirements (Lewis et al., 1961), have high fecundity, and show agonistic behaviors towards other species (Moyle 2002). Furthermore, flexible foraging strategies and a wide tolerance of poor water quality have made them keystone predators in many environments (Schindler et al., 1997). *Micropterus salmoides* have the ability to dramatically change pond trophic compositions through top-down effects (Keast and Web 1966; Carpenter and Kitchell 1993; Whittier and Kincaid 1999). Experimental and correlational studies indicate that predation by *Micropterus salmoides* reduces the density and species diversity of native and alien aquatic vertebrates and invertebrates and can cause trophic cascades in lentic environments (Maezono and Miyashita 2003; Maezone et al., 2005). *Micropterus salmoides* have been implicated as a preliminary reason for the extirpation of the federally endangered *Notropis topeka* (Topeka shiner) from streams in Kansas (Schrack et al., 2001). Furthermore, the changes in trophic compositions caused by *M. salmoides* may have led to the decline or local extirpation of some native California fish (Moyle 2002).

Other Amphibian Species of the Study Area

Bufo boreas halipois (California toad), *Pseudacris cadaverina* (California treefrog), and *Ensatina eschscholtzii eschscholtzii* (Monterey salamander) also occupied the study area. Although these amphibian species were present, their relative abundances and detectability were too low to reliably examine the influences of *M. salmoides*.

Anuran Predators Observed in Study Area

Potential *R. draytonii* and *P. regilla* predators that I observed in the study area include *Thamnophis hammondi* (two-striped gartersnake), *T. elegans* (terrestrial gartersnake), *T. sirtalis* (red-sided gartersnake), *Ardea herodias* (great blue heron), *A. alba* (great egret), *Egretta thula* (snowy egret), *Butorides virescens* (green heron), *Actitis macularia* (spotted sandpiper), *Procyon lotor* (raccoon), *Mephitis mephitis* (striped skunk), *Felis domestica* (feral cat), and *M. salmoides* (See Fellers 2005 and Rorabaugh and Lannoo 2005 for all references).

Additionally, predatory invertebrates including odonata (dragonflies and damselflies), hemiptera (giant water bugs and water boatman), and ephemeroptera (mayflies and allied taxa) were present in both ponds and have the potential to prey upon anuran larvae (Heyer et al., 1975; Smith 1983; Caldwell et al., 1980).

Furthermore, *R. draytonii* preys upon *P. regilla* (Hayes and Tennant 1985; USFWS 2005).

METHODS AND MATERIALS

Study Area

My study was conducted from 2006 to 2009 in two ponds on Cañada de la Pila Creek along the southern slope of the Santa Ynez Mountains within the Transverse Mountain Range in Santa Barbara County, California (UTM: 3819615/764710 Zone: 10S) (Figure 1). This property is owned by the County of Santa Barbara and is adjacent to the Tajiguas Landfill, which is operated by the County of Santa Barbara, Public Works Department, Resources Recovery and Waste Management Division. Both ponds were constructed in the 1980's to retain sediments released from adjacent landfill activities. The Tajiguas Landfill is permitted by four resource agencies (California Department of Fish and Game, U.S. Fish and Wildlife Service, the Army Corps of Engineers, and the California Regional Water Quality Control Board) to manage these ponds and periodically remove accumulated sediments. Sediment management in the ponds involves the removal of surface water and subsequent removal of sediments using heavy equipment. As mitigation for the potential effects of sediment removal, the resource agencies require the implementation of conservation measures for native anurans including the management of alien species.

The two ponds lie in a southern to northern orientation, similar to the orientation of Cañada de la Pila Creek, and are referred to as either the northern or southern pond. The two ponds are separated by a levee that is approximately 50 m

wide. Surface water is conveyed between the ponds by a 91.4 cm diameter corrugated metal culvert. Surface water connectivity between the ponds occurs only for a short time during and following storm events. The proximity of the ponds and the presence of the culvert facilitate the movement of juvenile and adult anurans between the ponds (personal observation). The ephemeral nature of the surface water conveyances between the ponds and annual timing of winter storms does not allow for the transmission of larval anurans.

The southern pond has more shoreline habitat, is deeper, and has a larger surface area than the northern pond (Figure 2). These conditions make the southern pond more persistent than the northern pond; the longer hydroperiod provides anuran breeding habitat even when the region experiences drought conditions (personal observation).

Open water habitats within the ponds support emergent vegetation including *Cyperus eragrostis* (nutsedge), *Scirpus californica* (California bulrush), and *Typha latifolia* (broad-leaved cattail). Aquatic vegetation predominately consists of *Elodea* sp (waterweed). The proximity of the ponds and land management activities has caused similar species compositions and a simple spatial heterogeneity of the emergent vegetation.

Upland areas immediately surrounding the ponds are dominated by native and non-native annual and perennial shrubs including *Xanthum strumarium* (cocklebur), *Ricinus communis* (castor bean), *Melilotus alba* (white sweet clover), and *Melilotus indica* (yellow sweet clover). Due to fluctuating water levels and

land management activities, these plants typically colonize the ponds during early succession.

Venturan coastal sage scrub occurs on the upper banks of the ponds. This community is dominated by native drought deciduous, soft-leaved species. Dominant species observed in these areas include *Baccharis pilularis* (coyote brush) and *Artemisia californica* (California sagebrush). Other plants that are commonly associated with this habitat type include *Hazardia squarrosa* (sawtooth goldenbush), *Calystegia macrostegia* (morning glory), *Lotus scoparius* (deer weed), *Leymus condensatus* (giant wild rye), *Rhus integrifolia* (lemonade berry), *Sambucus mexicana* (Mexican elderberry), *Toxicodendron diversilobum* (poison oak), and *Salvia melifera* (black sage).

Areas above Venturan coastal sage scrub are composed of a mosaic of *Ceanothus megacarpus* (big pod ceanothus) chaparral. Species in this vegetation community include *C. megacarpus*, *C. spinosus* (green-bark ceanothus), *Heteromeles arbutifolia* (toyon), *Malosma laurina* (laurel sumac), *Salvia melifera*, *Rhus ovate* (sugar bush), *Cerocarpus betuloides* (mountain mahogany), *Adenostoma fasciculata* (chamise), *Leptodactylon californicum* (prickly phlox), *T. diversilobum*, *Mimulus arantiacus* (sticky monkerflower), *Prunus ilicifolia* (holly-leaved cherry), *Clematis ligusticifolia* (clematus), *Marah macrocarpus* (wild cucumber), and *Erigonium fasciculatum* (California buckwheat). A number of rocky bluffs occur in these areas. Species commonly observed on these bluffs include *Selaginella* sp., *Pellaea andromedifolia* (coffee fern), *P. mucronata* (bird's foot

fern), *Polypodium californicum* (California polypody), and *Dudleya lanceolata* (lance-leaved dudleya).

Areas within Cañada de la Pila creek upstream of the ponds consist of *Quercus agrifolia* (southern coast live oak) riparian forest and central coast cottonwood-sycamore riparian forest. *Quercus agrifolia* riparian forest communities are dominated by *Quercus agrifolia* interspersed with individuals of *Umbellularia californica* (California bay) and *Platanus racemosa* (western sycamore). Other common species in this area include *Solanum xanti* (purple nightshade), *T. diversilobum*, *Symphoricarpos mollis* (snowberry), *Artemisia douglasiana* (mugwort), and *Stachys bullata* (wood mint). Wetland species that are found adjacent to the creek include *Equisetum* sp. (horsetail), *C. eragrostis* and *T. latifolia*.

Ruderal areas and scattered grasslands including roads and areas disturbed by land management activities occur adjacent to and south of the ponds. Due to their frequent disturbance, these areas are dominated mostly by non-native species including *R. communis*, *Carduus pycnocephalus* (Italian thistle), *Centaurea solstitialis* (yellow star thistle), *Silybum marianum* (milk thistle), *Hirschfeldia incana* (summer mustard), *M. alba*, *M. indica*, *Ehrharta* sp. (veldt grass), *Piptatherum miliaceum* (smilo grass) and other non-native annual and perennial grasses. Scattered, planted ornamental trees and shrubs also occur in these areas.

As is typical of regions with a Mediterranean climate, the majority of annual precipitation occurs between December through March. This precipitation pattern results in highly seasonal creek flows. Following these highly seasonal creek flows, the accumulation of water in the ponds provides anuran breeding opportunities. Except in years with significantly higher than average precipitation, the reaches of Cañada de la Pila upstream of the ponds do not have an adequate hydroperiod that supports anuran breeding; therefore, during typical years the vast majority of successful breeding occurs in the ponds.

During the 2006-2007 and 2008-2009 wet seasons, the region experienced a drought with below average annual rainfall (46 % of average in 2006-2007 and 91% of average in 2008-2009) (Santa Barbara Flood Control 2009). These conditions caused a reduction in the amount of water, shoreline habitat, and depth in the northern pond, which was unsuitable breeding habitat for *R. draytonii* (Rathbun 2005). However the 2007-2008 wet season was an above average precipitation year (132% of average in 2007-2008) and facilitated *R. draytonii* breeding in both ponds. *Pseudacris regilla* are fairly plastic in their breeding habitat requirements, have a relatively shorter developmental period (Rorabaugh and Lannoo 2005), and successfully reproduced in both ponds in 2007, 2008, and 2009. Due to the greater size and depth of the southern pond it maintained suitable anuran breeding habitat for both species during all survey years.

Micropterus salmoides Control and Eradication

To test whether the presence of *M. salmoides* limits the densities of the different life stages of *R. draytonii* and *P. regilla*, three *M. salmoides* control and/or eradication treatments were performed. One eradication treatment was performed in the northern pond in 2006, and two attempted eradication treatments were performed in the southern pond in 2007 and 2009, respectively. Due to the local scale of my study area, eradication treatments could not be assigned randomly.

In October 2006, *M. salmoides* in the northern pond was eradicated by removing all suitable fish habitat (surface water and underlying substrates) with a combination of a trailer-mounted 20.3 cm diameter water pump and an excavator (Caterpillar 330) equipped with a large excavation bucket. The eradication of *M. salmoides* in the northern pond made conditions in this pond suitable for comparisons with the southern pond, which supported a population of *M. salmoides* with variable abundances in 2007, 2008, and 2009.

In 2007, the first control attempt of *M. salmoides* was conducted in the southern pond. Control was achieved by removing the majority of all suitable fish habitat with a combination of a trailer-mounted 20.3 cm diameter water pump and an excavator (Caterpillar 330) equipped with a large excavation bucket. Surface water was removed in the pond between mid July to early October 2007. Following water removal, control through the use of the excavator was initiated in mid October 2007. *Micropterus salmoides* control activities involving the excavator included the excavation of a hole approximately 1.8 m in depth by 3.0 m in length

and width, proximate to the small, residual pool that remained after the majority of the water was removed. Following the excavation, a channel between the residual pool and the excavation was created. This channel facilitated the draining of the residual pool and transported the majority of the remaining fish into the excavation. The trailer-mounted water pump was then used to remove the majority of the water that accumulated in the excavation. The excavator was then used to remove the majority of the *M. salmoides* from the excavation, and place them in an upland area where their demise was ensured. Following the removal of the majority of the fish, the remaining excavation was filled in with dry sediments to ensure the demise of the remainder of the fish in the excavation. The 2007-2008 wet season had above average rainfall and the southern pond filled to capacity within three months of treatment.

In 2009, gill nets were used in a second attempt to eradicate the remaining *M. salmoides*. *Micropterus salmoides* eradication efforts with gill nets began in early January 2009 and continued for 10 weeks until early March 2009. Gill nets consisted of sinking monofilament experimental gill nets manufactured by Memphis Net. Nets ranged from 30 m to 36 m in length and were 1.8 m tall. Each net had six panels of varying lengths based on the total net length with mesh bar mesh sizes of 10 mm, 12.5 mm, 18.5 mm, 25 mm, 33 mm, and 38 mm. Initially, the panel with the smallest (10 mm) bar mesh size was set closest to the shoreline and the largest bar mesh size was set farthest out in the pond. Following the first week of net deployment, the panel with the smallest bar mesh size was removed

from the water and the remaining four panels with the larger bar mesh size remained submerged. This was performed to increase the effectiveness of the nets since the fork length of the *M. salmoides* (range 29.5 to 32.0 cm) was larger than the smallest bar mesh size could capture and no indications of successful *M. salmoides* reproduction (e.g., fry, fingerlings or juveniles) was observed in 2009. Gill nets were deployed with an oar-operated pontoon boat (a metal frame boat with two pontoons consisting of nylon-covered inner tubes generally manufactured for recreational anglers). Nets were anchored to shore with rebar sunk into the substrate and were positioned either perpendicular to shore or at an approximate 45° angle to shore. The pond end of the net was weighted with excess lead line, and a surface float with a 4.0 m cord was used to indicate the position of the net. Following weekly net checks and fish removal, nets were repositioned within 3.0 m of their original location. Following fork length measurement of the recovered fish, they were placed in an upland area to ensure their demise.

During *R. draytonii* and *P. regilla* translocation activities conducted in late October 2009 as part of the Tajiguas Landfill reconfiguration project (Santa Barbara County 2008), I captured with a dip net, measured, and dispatched a single juvenile *M. salmoides* in the southern basin. This capture confirmed that the *M. salmoides* population in the southern pond during the 2009 survey period consisted of a single juvenile fish.

Visual Encounter Surveys

For pond-breeding amphibians, visual encounter surveys are commonly used to estimate species densities (Crump et al., 1994; Olson et al., 1997). Visual encounter surveys typically reflect only the density in the preferred habitats of amphibians and not the actual density per total surface area of the study area (Crump et al., 1994; Olson et al., 1997). Visual encounter surveys are applicable to the populations of *R. draytonii* and *P. regilla* in the study ponds, because the majority of preferred anuran habitat occurs in these areas.

Surveys in 2007 were conducted after *M. salmoides* were eradicated in the northern pond, but prior to *M. salmoides* control efforts in the southern pond. Surveys in 2008 were conducted in both ponds following the first *M. salmoides* control effort conducted in the southern pond. Surveys in 2009 were conducted in both ponds when surface water was present and following the second control effort of *M. salmoides* in the southern pond.

Surveys were conducted one to four times every 10 days. This intensive sampling regime was designed to ensure the detection of all life-stages of anurans by accommodating for the seasonal and daily usage of lentic and riparian habitats by the two species throughout the annual survey periods. In 2007, day surveys (n = 19) and night surveys (n = 18) were conducted between 31 May and 14 August. In 2008, day surveys (n = 32) and night surveys (n = 23) were conducted between 27 April and 18 September. In 2009, day surveys (n = 12) and night surveys (n = 12) were conducted between 12 May and 21 July. Visual encounter surveys were

prematurely stopped in 2009 because the populations of *R. draytonii* and *P. regilla* were translocated to an adjacent watershed (Arroyo Quemado), approximately 1.2 km east of the study area, as part of the Tajiguas Landfill reconfiguration project (Santa Barbara County 2008).

Day surveys were utilized since these generate more accurate density estimates of larvae and metamorphs (USFWS 2005). Day surveys were conducted between sunrise and sunset. Night surveys generate more accurate density estimates of adults (USFWS 2005). Night surveys were conducted between sunset and 0000 hours. Often, multiple day and night surveys were conducted per survey day. For the analyses, I used the maximum number of each life stage of both anuran species recorded during any one survey date during the night or day, respectively. This provides a better measure of the densities of these species due to imperfect detections associated with visual encounter surveys.

Past land use activities, including the periodic removal of emergent vegetation and accumulated sediments, resulted in an abrupt transition (>0.5 m) from shallow to deep water in the ponds. These activities prevent high abundances of emergent wetland vegetation and create a shoreline with a distinct littorial (open water) to riparian zone (land). The abrupt shoreline transition, structurally simple wetland vegetation complexity and composition, and high water clarity of the study ponds resulted in potential high detectabilities of all life stages (larval, metamorph, and adult) of both *R. draytonii* and *P. regilla* within these areas.

Surveys were conducted by paddling an inflatable pontoon boat or by walking around the pond shorelines and focused on all visible underwater habitats within 1 m of the littoral zone and 1 m of the riparian zone (e.g., a 2 m wide transect). All surveys were initiated and stopped at a single location. Surveys were conducted in a linear fashion around the pond to reduce the risk of double counting individuals. During each survey, all available habitats within the 2 m transect were observed, and when necessary, with the assistance of 10x42 binoculars (Swift). At night, a <100,000 candle power light (Nite Lite) was used to detect anurans by the eye shine method (Corben and Fellers 2002). These survey methods provided the ability to accurately record individual *R. draytonii* and *P. regilla* from a distance (with binoculars and a light when necessary), thereby reducing disturbance to *R. draytonii*, a federally threatened species.

Anurans observed in the ponds were located underwater, partially-submerged along in the littoral zone, in vegetation, under cover, or in the open within the riparian zone. Each anuran observed was visually classified to life stage as larvae, metamorph, or adult. Adults were classified as belonging to cohorts from at least one year before the current survey year. Therefore, this classification encompasses both metamorphs from prior years that have not been recruited into the adult reproductive population and sexually mature adults. Metamorphs were classified as belonging to cohorts of the same year as the survey. Handling of anurans was precluded by the CDFG and USFWS regulations; therefore, I used my prior experiences with these species to make the life stage determinations.

Spatial Analysis

The amount of shoreline (in meters) was calculated once a week during the 2007, 2008, and 2009 survey periods (Figure 2). Using conspicuous landmarks surrounding the ponds, I used high-resolution aerial photos to hand-draw the shoreline. I then digitized the shorelines drawn on the aerial photos into ArcGIS (ESRI Redlands) geographic information system (GIS), and the amount of shoreline was then calculated using geo-referenced aerial photos in Terrasync (Trimble). For the descriptive anuran density comparisons, I standardized the anuran densities by summing the maximum number of anurans observed during day or night surveys within the 2 m transect and dividing these values by the amount of available shoreline (m) for the week when the respective survey was conducted.

Descriptive Comparisons

The unique land management activities, the rare species composition of my study area, and the local scale of my study prevented the establishment of suitable replicate ponds. This lack of replicates prohibited the design of an experiment that was suitable for statistical hypothesis testing (Zar 1999). Therefore, my results are strictly descriptive and observational.

To determine if the density of the different life stages of *R. draytonii* and *P. regilla* changed in response to the abundance of *M. salmoides*, I performed a number of descriptive comparisons between survey years in each respective pond

and between the ponds themselves when suitable habitat for each respective anuran species was present.

To perform these comparisons, the standardized anuran density results from the day or night surveys, respectively, recorded at each pond during each annual survey period were averaged and one value was used to compare anuran density across survey years or between the ponds. Additionally, the standardized anuran densities from the day or night surveys, respectively, recorded at the each pond during each individual survey day were used to determine if the densities of the different life stages of the anurans showed any patterns within the annual survey periods. For all comparisons, I used both day and night surveys in the comparisons, but comparisons were only made between each respective survey time and not between them.

To preclude comparing survey data obtained before the annual expected emergence of metamorphs of each species, I pooled survey years and excluded negative survey results obtained before the first annual positive survey result for this life stage. This technique precluded comparing portions of the annual survey periods when metamorphs were not expected to be present and potentially skewing the data. For *R. draytonii* metamorphs, the earliest annual date they were detected was 1 July 2009, and for *P. regilla* metamorphs, the earliest annual date they were detected was 17 June 2008. Therefore, all data collected prior to these dates have been excluded from these comparisons. This technique was not applied to larvae or

adults since they were expected to be present in the ponds prior to the annual initiation of surveys and throughout the annual survey period.

Micropterus salmoides were successfully eradicated in the northern pond in 2006; therefore, I performed descriptive comparisons between the annual average densities of all life stages of *R. draytonii* in the northern pond and the southern pond for day and night surveys conducted in 2008. I performed descriptive comparisons between the northern and southern ponds in 2008 only, because an adequate hydroperiod conducive for successful larval metamorphosis in the northern pond was not present in 2007 or 2009. For larval and adult *P. regilla* I performed descriptive comparisons between the annual average densities in the northern pond and southern pond for all survey years. Due to complete drying of the northern pond in 2009 before the annual expected emergence of *P. regilla* metamorphs, comparisons of *P. regilla* metamorphs were not made between the two ponds. Therefore, *P. regilla* metamorph density comparisons between the two ponds were only performed for 2007 and 2008.

RESULTS

Micropterus salmoides Control and Eradication

The *M. salmoides* eradication attempt conducted in 2006 in the northern pond was successful. I observed no *M. salmoides* in the northern pond during visual encounter surveys in 2007, 2008, and 2009. Both eradication attempts in the southern pond conducted in 2007 and 2009 were unsuccessful, but each attempt resulted in a significant reduction of the *M. salmoides* population during the 2008 and 2009 survey periods (Figure 3).

In 2007, the population of *M. salmoides* in the southern pond consisted of approximately 3,000 individual fish of all life stages (fry, juvenile and adult) (Figure 3). As a result of the 2007 eradication attempt, the population of *M. salmoides* was controlled and drastically reduced to ten juvenile fish (Figure 3). Throughout the 2007 control activities, sources of groundwater percolation continued to recharge the lower elevational areas of the southern pond, so the excavator was used to block these sources. This measure was effective at reducing the majority of groundwater percolating into the suitable areas of *M. salmoides* habitat, but proved unsuccessful in the elimination of all suitable fish habitat. Unfortunately in July 2008, I detected a small population of *M. salmoides* in the southern pond. It appears that the physiological tolerance of *M. salmoides* fry and fingerlings to low dissolved oxygen levels and high water temperatures (Coutant

1975; Smale and Rabeni 1995) allowed them to persist in the small areas of refugia recharged by groundwater (Alvarez et al., 2003).

Between January and March 2009 nine additional juvenile *M. salmoides* were removed from the southern pond with gill nets (Figure 3). The *M. salmoides* removed in 2009 had an average fork length of 31.0 cm (range 29.5 to 32.0 cm). Although, *M. salmoides* survived throughout the 2009 breeding period of *P. regilla* and *R. draytonii*, gill netting activities drastically reduced the *M. salmoides* population to 0.1 of their 2008 population size (Figure 3). In October 2009, a single juvenile *M. salmoides* in the southern pond was captured, measured, and dispatched. This juvenile had a fork length of 36.8 cm. Following this capture, no additional *M. salmoides* were observed in the southern pond.

Anuran Densities

My annual average day and night survey results for adult *R. draytonii* from the southern pond show no discernable pattern (Figure 4A). Additionally, survey results for day and night surveys conducted on each survey day show no discernable pattern (Figure 5). Very low adult densities were recorded during day surveys for all survey years (Figure 4A) and all survey days (Figure 5). These results were anticipated since adults are predominately nocturnal (USFWS 2005). Furthermore, adult *R. draytonii* annual average density (Figure 4A) and individual survey day densities (Figure 5B) recorded during 2007 and 2008 night surveys are similar;

however, there is a marked increase in the adult density recorded during the 2009 night surveys.

For metamorph *R. draytonii*, the average annual density recorded in the southern pond indicate that the day and night survey results for both 2007 and 2008 are similar, but there is a salient increase in their density during both day and night surveys conducted in 2009 (Figure 4B). Additionally, I recorded low *R. draytonii* metamorph densities during day and night surveys for each survey day in 2007 and 2008 and higher densities in 2009 (Figure 6). The density of *R. draytonii* metamorphs progressively increases throughout the 2009 survey period (Figure 6). For larval *R. draytonii*, I recorded a similar pattern of annual average (Figure 4C) and survey day (Figure 7) densities during both day and night surveys, including a conspicuous increase in 2009.

My results for day and night surveys for the annual average adult *R. draytonii* densities between the northern and southern pond in 2008 indicate that they were similar (Figure 8A). Additionally, survey results for each survey day show no discernable pattern (Figure 9). My results for day and night surveys indicate that there was an evident difference between the annual average density of both larval (Figure 8B) and metamorph (Figure 8C) *R. draytonii* between the ponds. Furthermore, survey results for each survey day show a similar pattern (Figure 10 and Figure 11).

In the southern pond, I recorded very low densities during day and night surveys for all *P. regilla* life stages in the average annual densities (Figure 12) and

densities for each survey day (Figure 13, Figure 14, and Figure 15). Although there were low recorded average densities across survey years and on each survey day, both adults (Figure 12A and Figure 13) and metamorphs (Figure 12B and Figure 14), showed a slight, yet steady increase between 2007 through 2009. For adults, this increase was recorded during night surveys (Figure 12A and Figure 13B) and was recorded for juveniles during both day and night surveys (Figure 12B and Figure 14). The low densities of adult *P. regilla* recorded during day surveys were anticipated since adults are predominately nocturnal (Rorabaugh and Lannoo 2005). Low larval densities were recorded in the annual average (Figure 12C) and for each survey day (Figure 15) during both day and night surveys in 2007 and 2009, and a relatively higher density of larvae was recorded in both day and night surveys in 2008.

My annual average results (Figure 16) and results for each survey day (Figure 17, Figure 18, and Figure 19) for comparisons between the northern and southern pond indicate that the northern pond consistently supported relatively higher adult, metamorph, and larval *P. regilla* densities. Adults showed relatively higher densities in the northern pond during night surveys conducted in 2007 and 2008 (Figure 16A and Figure 17). Additionally, their 2009 density in the southern pond exhibits an increase from densities recorded in 2007 and 2008 to levels that are similar to the density recorded in the northern pond in 2008 (Figure 16A and Figure 17). For adults, this trend is evident only during night surveys (Figure 16A), which was expected since adults are predominately nocturnal (Rorabaugh and

Lannoo 2005). Metamorphs exhibited a similar pattern of higher relative densities in the northern pond (Figure 16B) and on each survey day (Figure 18) in 2007 and 2008, but relatively higher densities were detected during day surveys. Larval *P. regilla* exhibited relatively higher densities in the northern pond across survey years (Figure 16C) and on each survey day (Figure 19), with higher densities recorded during day surveys. However, relatively fewer larvae were recorded in the northern basin in 2008 (Figure 16C and Figure 19).

DISCUSSION

I acknowledge that the rarity of the species assemblage and the specific land management activities of my study ponds limited the ability to find replicate ponds that were appropriate for *M. salmoides* control efforts. This lack of suitable replicates constrained the development of an experiment suitable for statistical hypothesis analysis (Zar 1999). These constraints limit my ability to generalize the influences that *M. salmoides* has on *P. regilla* and *R. draytonii* populations within the Transverse Mountain Range of southern California; however, my study has biological relevance about how *M. salmoides* influence *P. regilla* and *R. draytonii* populations at a local scale.

My results for adult *R. draytonii* may provide tentative support that juvenile *M. salmoides* did not influence the density of this life stage. Adult *R. draytonii* densities do exhibit an increase in the southern pond between the 2008 and 2009 survey years; however, this increase is not believed to be an artifact of the reduction of *M. salmoides* that occurred during this same period (Figure 4A). The factors influencing this marked increase are difficult to interpret, but this noticeable increase is believed to have been influenced by the lack of suitable adult *R. draytonii* habitat in the northern pond during the 2009 survey period that may have caused the adults to become more localized at the only area of available habitat. This claim is supported by similar average annual adult densities recorded in 2008 in the northern pond (0.026) and southern pond (0.028) when both ponds supported

similar habitat characteristics (Figure 5A). Furthermore, the pooled annual average adult densities for both ponds in 2008 (0.053) is very similar to the adult density recorded in the southern pond in 2009 (0.049), potentially indicating that the adult population size at my study area remained fairly constant. *Micropterus salmoides* predation on the adult life stages is not suspected because they are gape-limited predators and the largest *M. salmoides* captured had a fork length of 36.8 cm which is too small to successfully consume an adult *R. draytonii* with a snout-to-urostyle length between 85 to 138 mm (Jennings and Hayes 1994).

Consistent with other studies on the interactions of California ranids and alien fish, I found that the densities of larval and metamorph *R. draytonii* are influenced by the presence of *M. salmoides*. The low annual average densities of metamorph (Figure 4B) and larval (Figure 4C) *R. draytonii* recorded in the southern pond in 2007 and 2008, is believed to be a result of the influences of *M. salmoides*. This is supported with low densities recorded on each survey day for metamorphs (Figure 7) and larvae (Figure 8) during the same years. In the southern pond during the 2007 survey period, there were over 3,000 *M. salmoides* of all age classes and there were 10 juvenile *M. salmoides* during the 2008 survey period (Figure 3). In 2009, the population of *M. salmoides* had been reduced to a single juvenile (Figure 3). Consistent with the reduction in *M. salmoides*, I recorded a noticeable increase in the densities of both *R. draytonii* metamorphs and larvae. The inverse relationship between the number of *M. salmoides* and metamorph and larval *R. draytonii* densities appears to indicate that the control of *M. salmoides* caused a

notable increase in the density of these life stages. Additionally, it appears that the population of 10 juvenile *M. salmoides* was large enough to reduce the densities of these two life stages, but that the influence of a single juvenile *M. salmoides* was not strong enough to maintain a similar influence. I also recorded a progressive increase of metamorph *R. draytonii* recorded throughout the 2009 survey period, which may be explained by an increase in the density of this life stage as the larvae developed into metamorphs (Figure 10).

Further evidence of the influences of *M. salmoides* on these life stages is indicated by the large difference in their densities between the southern and northern pond recorded in 2008 (Figure 9B, Figure 9C, Figure 11, and Figure 12). The low recorded densities of metamorph and larval *R. draytonii* recorded in the southern pond in 2008 is believed to be an artifact of the influence of *M. salmoides*. In the southern pond during the 2008 survey period, there were 10 juvenile *M. salmoides* (Figure 3), which presumably reduced the densities of these two life stages. The difference in the number of *M. salmoides* and the densities of metamorph and larval *R. draytonii* between the ponds appears to indicate that in the absence of *M. salmoides* these two life stages sustained relatively higher densities. These results also lend support that the population of 10 juvenile *M. salmoides* in the southern pond in 2008 was large enough to reduce the densities of these two life stages.

The movement of metamorphs between watersheds near my study area could have been responsible for the differences in densities recorded in the northern

and southern pond in 2008 (Figure 8B and Figure 10) and in the southern pond during the annual survey periods (Figure 4B and Figure 6). However, it remains unknown if this life stage has the ability to traverse such distances over habitats with such variable topographies, land management regimes, and cover. I observed that the vast majority of recently-metamorphosed *R. draytonii* stay close to their natal waters and movements of this life stage usually coincide with periods of precipitation. During the annual survey periods, there were no significant rain fall events and I did not observe many metamorphs more than a few meters from their natal waters. Furthermore, it appears that there was little exchange of individual metamorphs in 2008 between the northern and southern pond when there was a distinct difference in metamorph densities between the ponds (Figure B). Consistent with the increase in metamorphs there was also a marked increase in the number of larval *R. draytonii* in the southern pond when it contained a single juvenile *M. salmoides* and in the northern pond when suitable *R. draytonii* habitat was present. The presence of higher densities of larvae presumably resulted in an increase of metamorphs as the larvae developed into this life stage. Therefore, I believe that the conspicuous increase in metamorph density recorded in the southern pond in 2009, and the apparent difference of larvae and metamorph densities between the northern pond and southern pond in 2008 is representative of the absence or low number of *M. salmoides*, and not indicative of the movement of metamorphs between my study ponds or local watersheds. However, there may have been movements of reproductively mature adult *R. draytonii* between my

study ponds and emigration and immigration of adults from adjacent watersheds. This may have influenced the relative reproductive output of the adult population, and resultantly manipulated the recorded densities of larvae and metamorphs observed between survey years.

Similar results to those exhibited by *R. draytonii* metamorphs and larvae were recorded for *P. regilla* adults and metamorphs at my study ponds. Low densities were recorded in both ponds during day and night surveys for all *P. regilla* life stages. Despite the low annual average and daily densities recorded in the southern pond, adults (Figure 12A and Figure 13) and metamorphs (Figure 12B and Figure 14) exhibit a gradual increase during the 2007 through the 2009 survey periods. This gradual increase coincides with the substantial reduction of the population of *M. salmoides* in the southern pond throughout this period. The results for larval *P. regilla* in the southern pond show a different pattern with relatively higher densities recorded during both day and night surveys conducted in 2008 (Figure 12C and Figure 15).

My results for the annual average (Figure 16) and results for each survey day (Figure 17, Figure 18, and Figure 19) also indicate that in comparisons between both ponds, the northern pond consistently supported relatively higher adult, metamorph, and larval densities. Interestingly, the density of adult *P. regilla* recorded in the southern pond in 2009 is similar to their density recorded in the northern pond in 2008 (Figure 16A and Figure 17). Similar to the adults, results for metamorph (Figure 16B and Figure 18) and larval (Figure 16C and Figure 19) *P.*

regilla exhibit a similar trend. However, I recorded lower larval densities in the northern pond in 2008 (Figure 16C and Figure 19). These results lend additional support to trends observed in the southern pond across survey years, which may be an artifact that in the absence of *M. salmoides* the northern pond supported higher densities of *P. regilla*.

The relatively higher density of *P. regilla* larvae observed in the southern pond and northern pond during day and night surveys in 2008 was not consistent with what I had anticipated. I had anticipated that along with the increase recorded for adult and metamorph densities there would be a similar increase in larval density. It is possible that the detectability of larval *P. regilla* was lower than the other life stages recorded, or when available, *P. regilla* larvae select water depths that exceed 1.8 m (Weitzel and Panik 1993), which was deeper than what was available along the majority of the littoral portion of the 2 m transect in the southern pond.

It is possible that the low detectability of *P. regilla* may be one factor that influenced the low recorded densities of *P. regilla*. I observed relatively more *R. draytonii* in the water or in open areas of the shoreline when compared to observations of *P. regilla*. *Pseudacris regilla* adults and metamorphs are relatively more terrestrial than *R. draytonii* and often seek refuge amongst low shrubs or in cool retreats (Knapp 1996; Schaub and Larsen 1978). These habits may have reduced the potential that I recorded adults and metamorphs on low shrubbery or in cool retreats. Additionally, larvae are often found in water deeper than 1.8 m

(Weitzel and Panik 1993) and they may not have occurred frequently in the 2 m transect that predominately did not contain water depth greater than 1.8 m.

Although my results for *P. regilla* should be applied conservatively due to the low densities recorded and low potential detectability of the species, they provide tentative evidence that the control or eradication of *M. salmoides* influenced this population of *P. regilla*.

It appeared that *R. draytonii* populations quickly rebounded following the eradication or significant reduction of *M. salmoides*. The reproductive output of the resident adult *R. draytonii* population potentially provided the source for the rapid rebound in the larval and metamorph life stages. Furthermore, there may have been immigration of adult *R. draytonii* from adjacent watersheds (Fellers 2005; Bugler et al., 2003; Fellers and Kleeman 2007; Tatarian 2008; Rathbun et al., 1997; personal observation), which could have been an additional source for this rapid rebound.

Pseudacris regilla populations did not show a similar rebounding effect. Prior to the initiation of my study, it is possible that the adult population of *P. regilla* was severely reduced by the influences of *M. salmoides* and there may not have been a large enough adult population to stimulate a comparative rebound in the larval and metamorph life stages. The duration of my study would not have been able to detect a population rebound if it is a relatively slower process in *P. regilla*. The recovery of anurans in lentic environments may be a slow process that may depend on the vulnerability of the anurans to the influences of the alien fish or on the length of time the alien fish have persisted in the habitat before they were

reduced or eliminated (Knapp et al. 2001). Weitzel and Panik's (1993) long-term study showed that *P. regilla* populations fluctuate widely and that the species is resilient to many habitat disturbances and predation. *Rana draytonii* adults and metamorphs also prey upon adult and metamorph *P. regilla*, which may be an additional top-down effect influencing the low recorded densities of this species (Hayes and Tennant 1985; USFWS 2005).

The relatively smaller response of the *P. regilla* population to the control and eradication of *M. salmoides* conducted on such a small scale should not diminish the concern over *M. salmoides* introduction into their habitat, but may exemplify a need to investigate their relationship over a larger spatial scale with longer study duration. Unfortunately, examining the long-term trajectory of the anuran populations following the eradication of *M. salmoides* is not possible at my study area since the populations of *R. draytonii* and *P. regilla* were translocated to an adjacent watershed in mid-2009 and the ponds will be converted into a concrete-lined trapezoidal channel (Santa Barbara County 2008). If future studies are conducted to investigate the influence *M. salmoides* control efforts have on native anurans, it would be best to conduct such studies over a larger scale within protected areas where land management activities remain fairly constant so the mechanisms responsible for the long-term trajectories of anuran populations could be determined. These studies may be important since potential amphibian stressors are unlikely to be evenly distributed across a species' range (Davidson 2004; Fisher and Schaffer 1996; Knapp et al., 2007). *Rana draytonii* and *P. regilla* may have

varying susceptibilities to these potential anuran stressors and genetically divergent populations within this range may have varying vulnerabilities (Knapp et al., 2007). Additionally, the use of laboratory trials and field enclosure experiments may elucidate the direct, indirect, and synergistic influences caused by *M. salmoides* to *R. draytonii* and *P. regilla*. The combination of these studies conducted with varying spatial and duration components may provide a better understanding of the proximate mechanisms responsible for these influences.

Antipredator adaptations in these species have been poorly studied, but it has been suggested that *R. aurora* and *P. regilla* larvae lack adaptations for coexistence with alien fish (Adams 2000). Although both species evolved in the presence of native fish, the antipredator responses to the native species may not be sufficient to allow coexistence with this alien species (Gamrat and Kats 1996). It is possible that there was a combination of predation (Vredenburg 2004; Pope 2008; Knapp and Matthews 2000), competition (Adams 2000), behavioral modifications (Lawler et al., 1999; Kupferburg 1997), or trophic influences (Heyer et al., 1975; Smith 1982; Caldwell et al., 1980; Adams 2000) or synergisms between these factors that influenced my results.

Evidence from my study that supports that predation may have been the main factor responsible for the changes in anuran densities comes from the observation of adult *P. regilla* in the stomach contents of two of four *M. salmoides* collected in late-2006. Although I have no direct evidence to support that *M. salmoides* preyed upon larval and metamorphic *R. draytonii*, *R. aurora* larvae are

palatable to fish and are readily preyed upon by *M. dolomieu* (Kiesecker and Blaustein 1998). Furthermore, Alvarez et al.,(2003) suggested that the increases in *R. draytonii* observed following the experimental removal of a multitude of alien fish, including *M. salmoides*, is a result of a reduction of predation on the metamorph and larval life stages. Additional evidence for rapid predation by alien fish comes from multiple experimental studies that show the abundance of conspecific anurans is reduced in the presence of alien fish through predation (Knapp and Matthews 2000; Vredenburg 2004; Pope 2008).

Besides predation, *M. salmoides* may have caused a trophic cascade reducing larval food availability which may have increased interspecific and intraspecific competition or caused behavioral modifications further reducing their populations (Adams 2000). The presence of *M. salmoides* may have caused a reduction in foraging activity resulting in slower growth rates, reduced biomass at metamorphosis, and may have increased their susceptibility to predation (Kiesecker and Blaustein 1998; Lawler et al., 1999). Modified trophic influences including fluctuations in predation rates by native predacious aquatic invertebrates may have also been a factor (Heyer et al., 1975; Smith 1982; Caldwell et al., 1980). I observed potential indications of predation by native aquatic invertebrates on *R. draytonii* metamorphs and larvae. The suspected victims of attempted invertebrate predation had fresh wounds including missing limbs, limbs missing portions of skin, or had lacerations that were not consistent with other recorded malformations within the *R. draytonii* population that appeared similar to infection by the parasitic

trematode (*Ribeiroia ondatrae*) (Johnson and Lunde 2005). Injuries caused by predacious aquatic invertebrates can also decrease the growth of larval anurans (Wilbur and Semlitsch 1990; Parichy and Kaplan 1990); however, these injuries were only observed in the southern pond in 2009 when there were high densities of larvae and metamorph *R. draytonii* and a single juvenile *M. salmoides*. This may be indicative of a reduction in predation by *M. salmoides* on the aquatic invertebrates that may have resulted in an increase in the density and species diversity of aquatic predaceous invertebrates in the southern pond in 2007 and 2008 (Maezono and Miyashita 2003; Maezone et al., 2005). Lastly, it is possible that *M. salmoides* transmitted an infectious agent to the anuran populations at my study ponds (Kupferburg 1995; Kiesecker et al., 2001), but no obviously diseased *M. salmoides* or anurans were found.

Management activities in the ponds have reduced the habitat structure, and subsequently may have exposed the native anurans to greater predation pressures (Pilliod and Peterson 2001) or indirect effects caused by the presence of the predator (Lawler et al., 1999). Lentic environments with a more complex spatial heterogeneity may assist in the mitigation of some of these effects by providing greater areas of embryo, larval, and metamorph refugia. It has been suggested, that the presence of emergent vegetation may provide suitable refugia for *R. aurora* in the presence of *M. dolomieu* (Kiesecker and Blaustein 1998); however, land management activities at my study site prevent the long-term establishment of emergent vegetation in the ponds. This lack of spatial heterogeneity and larval and

metamorph refugia may have exacerbated the influences of *M. salmoides* on *P. regilla* and *R. draytonii*.

Populations of native species may decline if alien species affect their recruitment. This phenomenon may be exacerbated when the native species has a life history that involves a multitude of life stages. In the case of the adult *R. draytonii* population, the identified top-heavy age structure recorded during the 2007 and 2008 survey periods may be indicative of insufficient recruitment and a declining population (Alexander 1958; Browne and Hecnar 2007). The presence of *M. salmoides* reduced the density of *R. draytonii* larvae and metamorphs and *P. regilla* adults, metamorphs, and larvae. This reduction in the densities of the early life stages of *R. draytonii* and all life stages of *P. regilla* likely led to a dearth of metamorphs being recruited into the adult populations (Pope 2007; Alvarez et al., 2003; Lawler et al., 1999). The potential reduction of metamorph recruitment may have eventually led to severely reduced anuran populations or the extirpation of one or both species at my study site. The extirpation of one or both anuran populations may have resulted if the adult populations were further reduced by a combination of natural mortality, lack of additional *M. salmoides* control efforts, land management activities (USFWS 2002), reduced connectivity with other anuran populations leading to the absence of immigration of individuals from adjacent populations (Pilliod and Peterson 2001; Knapp and Matthews 2001; Bradford et al., 2003; Hanski and Simberloff 1997), and in the case of adult *R. draytonii* the increased

potential of *M. salmoides* depredations as the *M. salmoides* grew larger enough to prey upon them.

The ephemeral nature of surface water in the northern pond may have provided the opportunity for successful anuran metamorphosis by periodically eliminating *M. salmoides* through drying of the pond followed by favorable biotic and abiotic environmental conditions, yet disallow the repeated introduction of *M. salmoides*. Therefore, the erratic hydrological nature of the northern pond may have acted as a relatively more secure area of *R. draytonii* and *P. regilla* metamorph recruitment if *M. salmoides* control efforts were not undertaken. This would not be a sufficient measure to rely upon if attempting to conserve the anuran populations at my study area since a unique combination of timing and environmental conditions would be required for the northern pond to provide this potential source of juvenile recruitment.

Although a number of factors have been implicated in the decline of *R. draytonii* and *P. regilla* populations, my results suggest that the presence of *M. salmoides* may reduce the populations of these species. Although my results are suggestive and not conclusive, they may be used as tentative evidence that the control or eradication of *M. salmoides* may be used to conserve *R. draytonii* and *P. regilla* populations at a local scale. My results may also motivate simple land management modifications to reduce or prevent the introduction of *M. salmoides* into the habitats of these two species. Any implemented *M. salmoides* control, eradication, or introduction prevention program implemented in the sympatric range

of *R. draytonii* or *P. regilla* may increase the availability of suitable reproductive habitat for these species. This increase in reproductive habitat may influence metapopulation dynamics; reduce population isolation; assist in increasing juvenile recruitment; provide a buffer against anthropogenic influences, stochastic fluctuations, or disease outbreaks; and confer overall conservation benefits to these species.

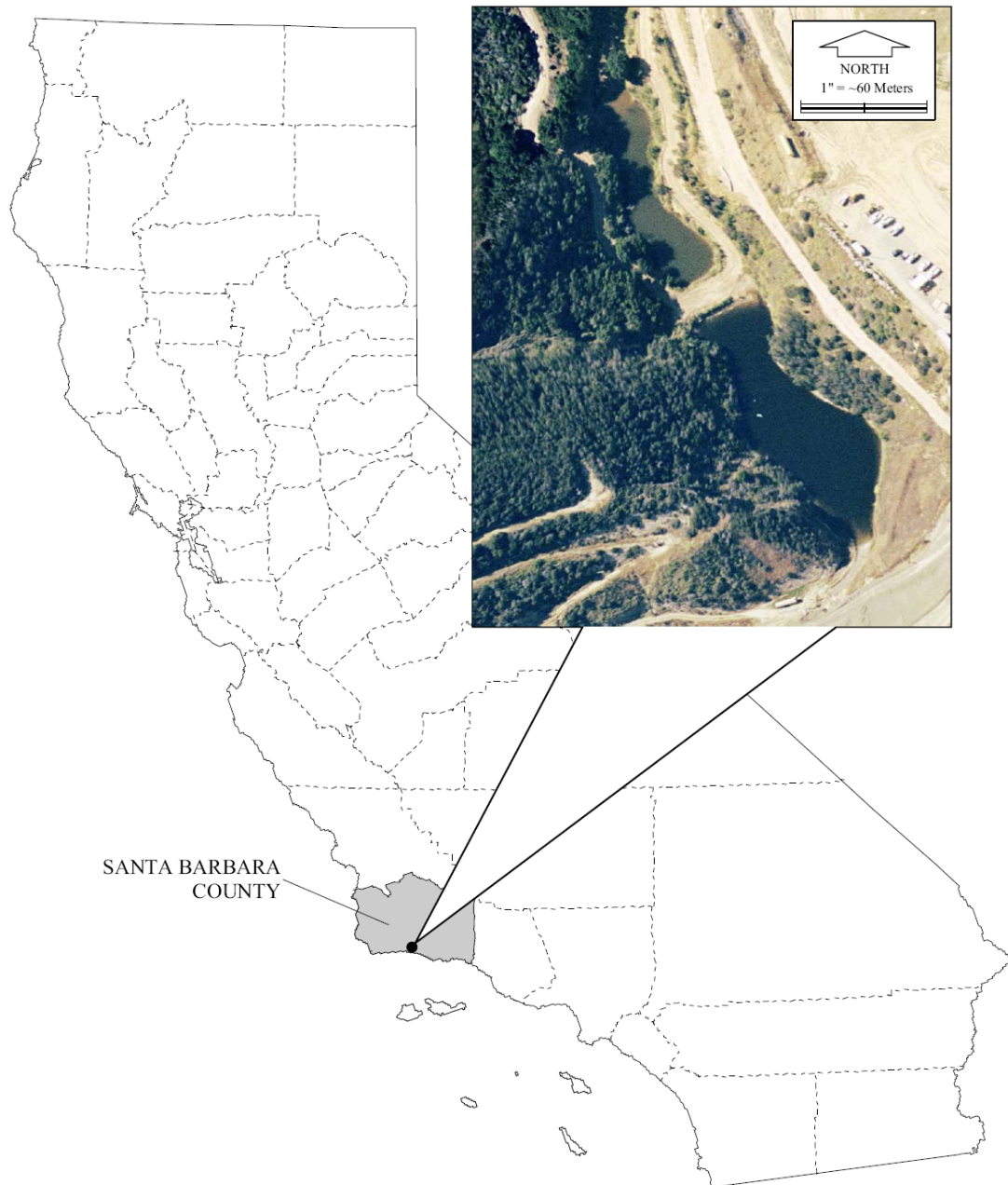


Figure 1: Map of the study area and aerial view of the northern and southern ponds in Santa Barbara County, California.

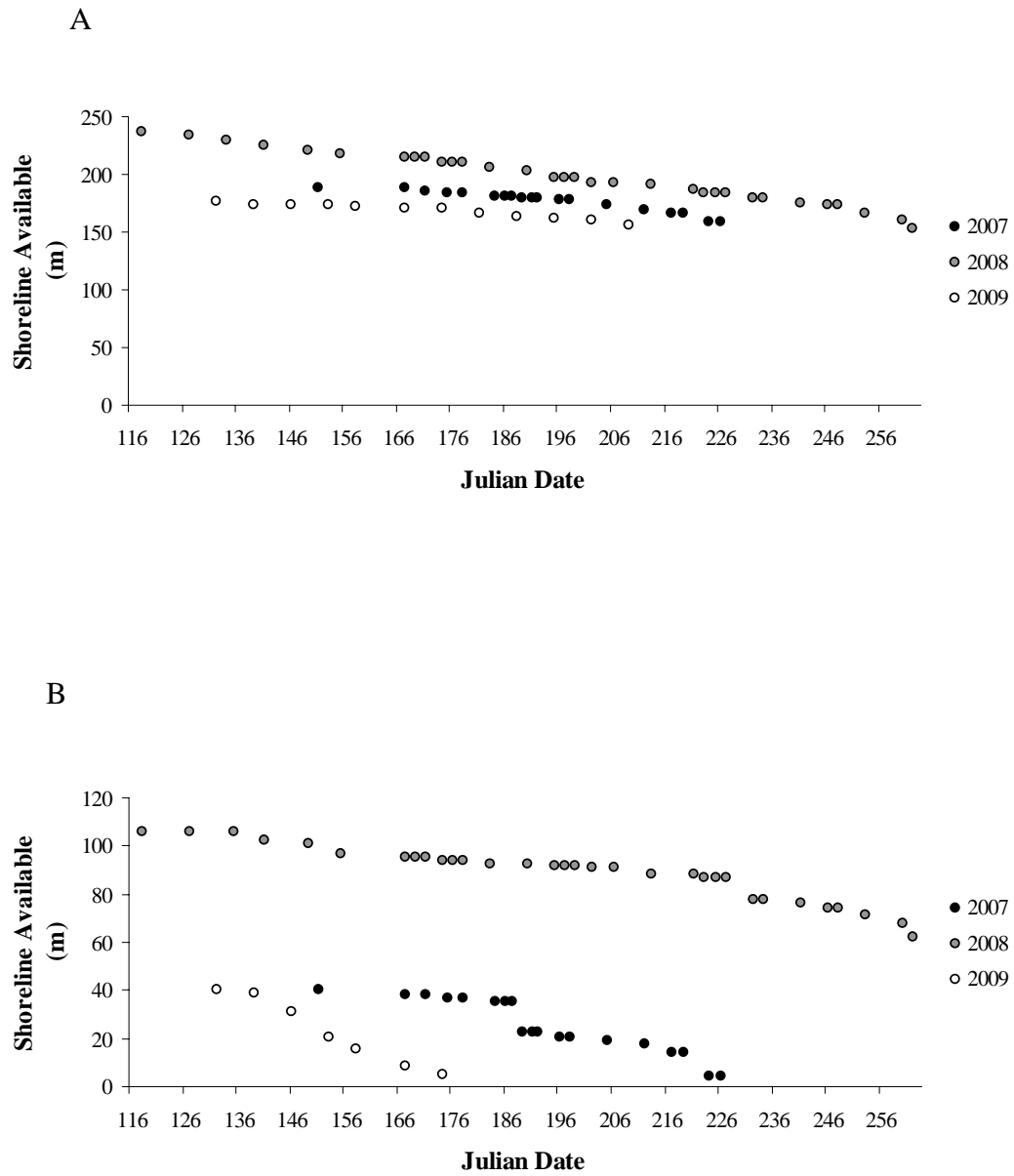


Figure 2: Shoreline availability data for the southern (A) and northern (B) pond during the 2007, 2008, and 2009 survey periods.

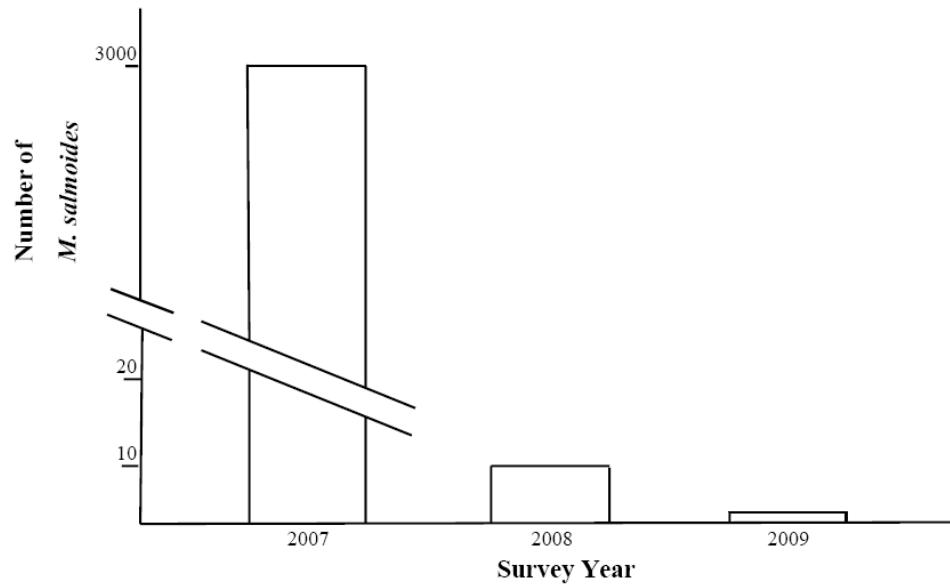
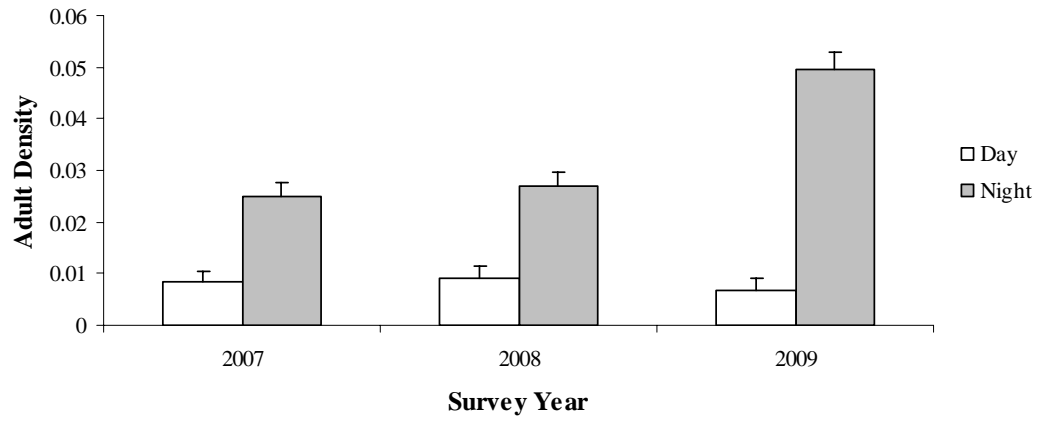
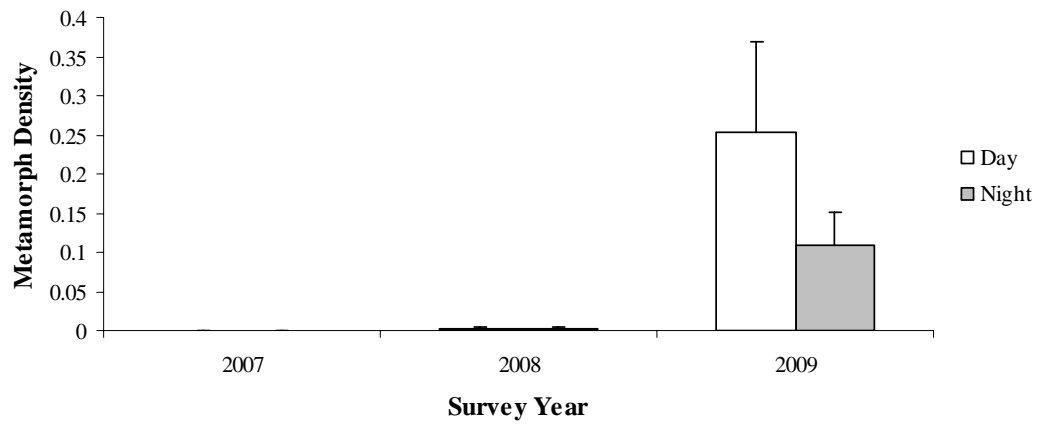


Figure 3: Number of *M. salmoides* recorded in the southern pond during the 2007, 2008, and 2009 survey periods.

A



B



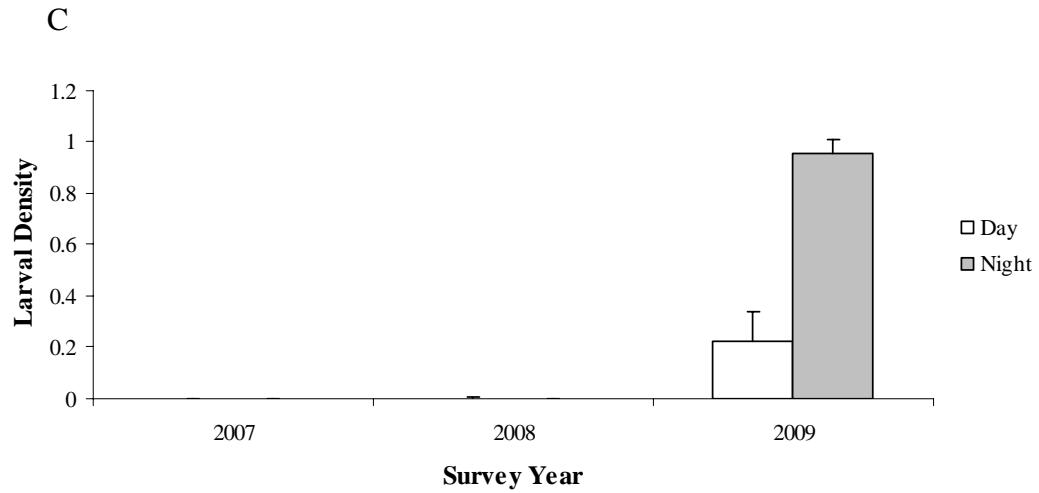


Figure 4: Comparisons of the average adult (A), metamorph (B), and larval (C) *R. draytonii* densities in the southern pond recorded during day and night surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods. Error bars represent the standard error.

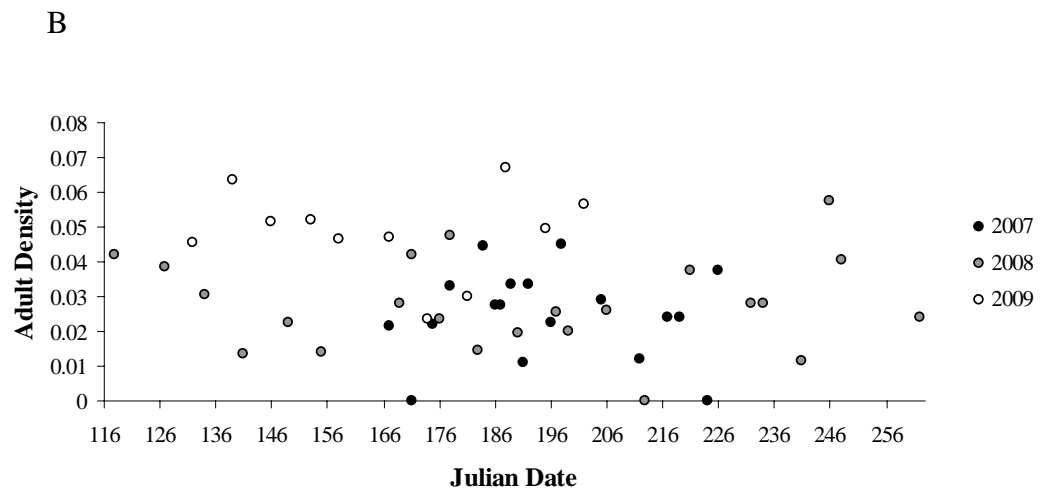
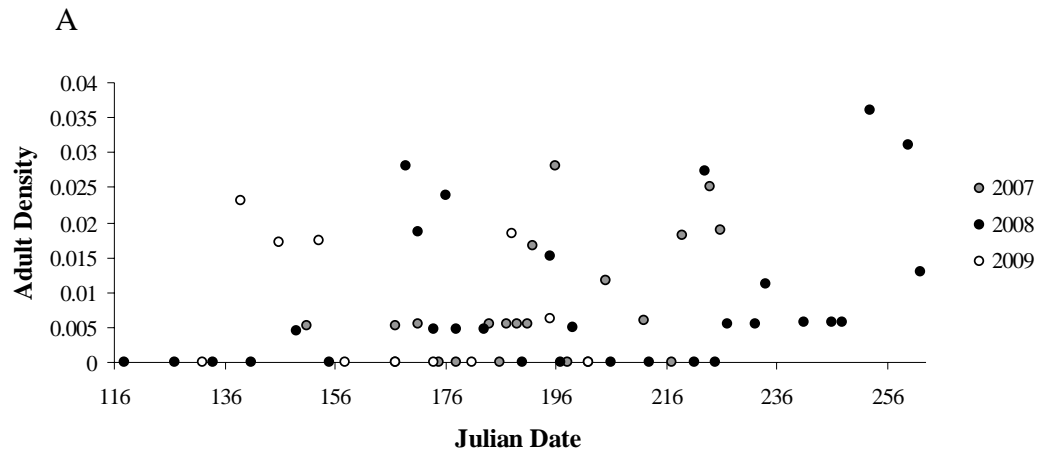


Figure 5. Densities of adult *R. draytonii* in the southern pond recorded during day (A) and night (B) surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods.

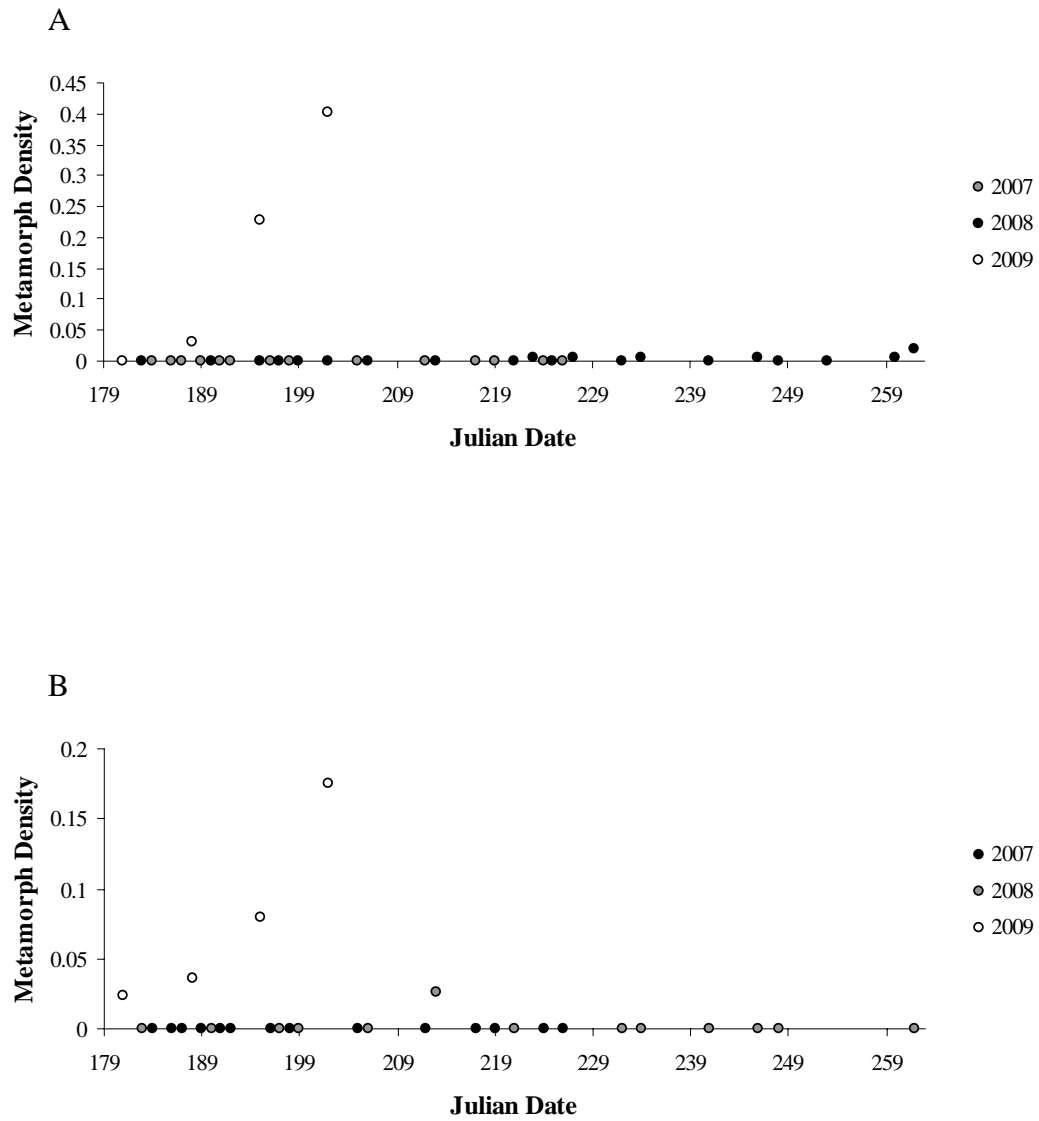


Figure 6. Densities of metamorph *R. draytonii* in the southern pond recorded during day (A) and night (B) surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods.

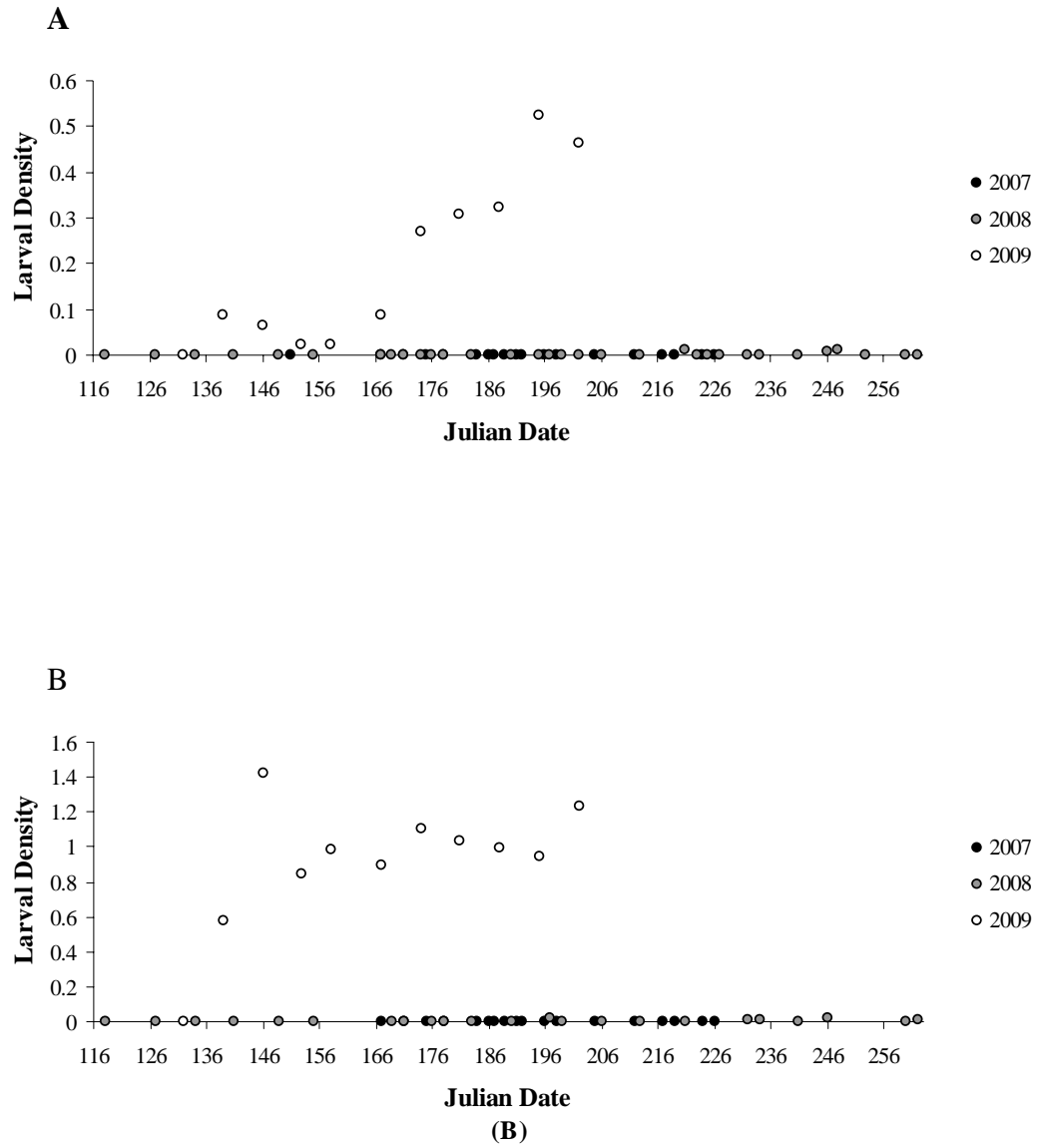
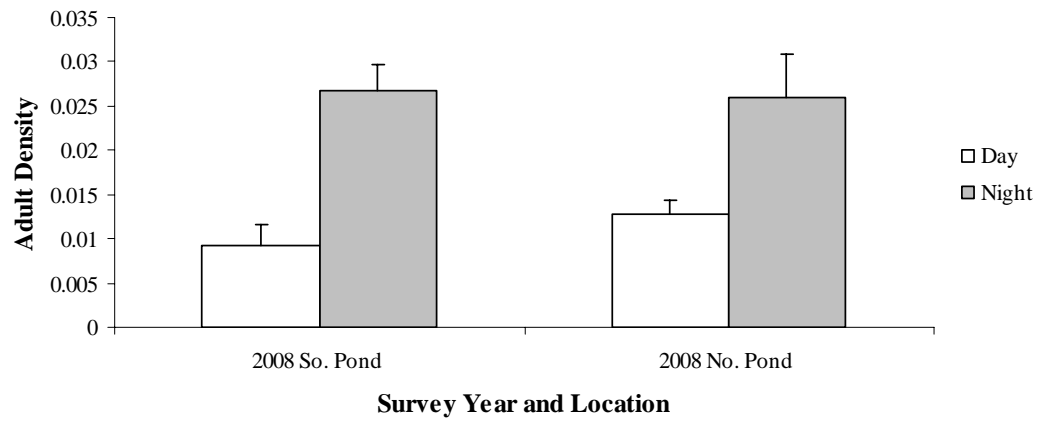
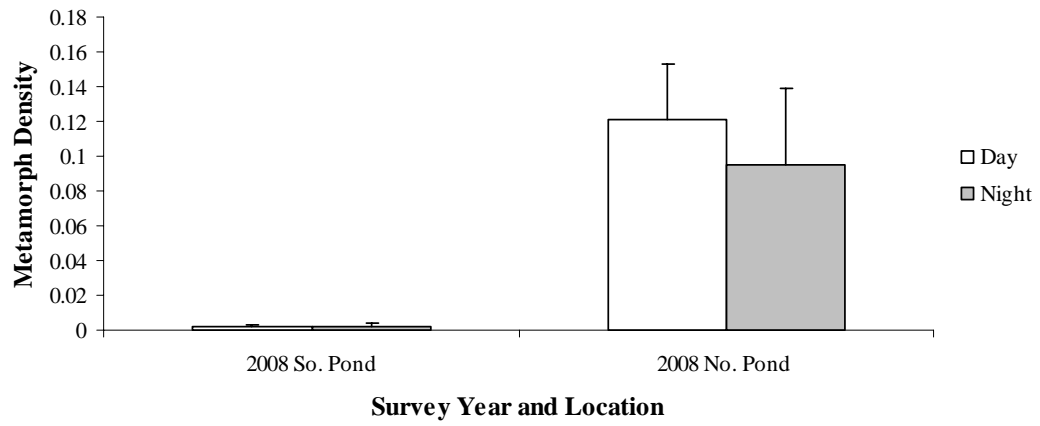


Figure 7. Densities of larval *R. draytonii* in the southern pond recorded during day (A) and night (B) surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods.

A



B



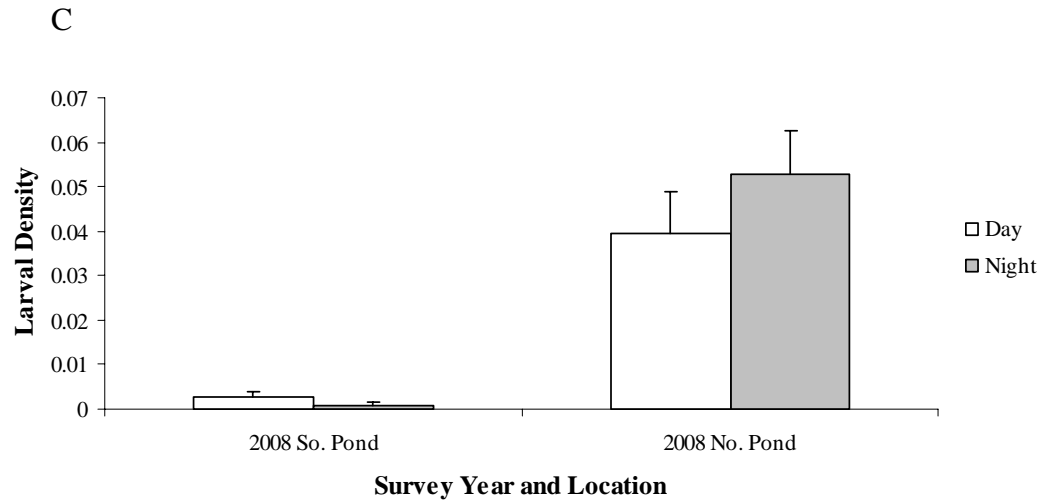
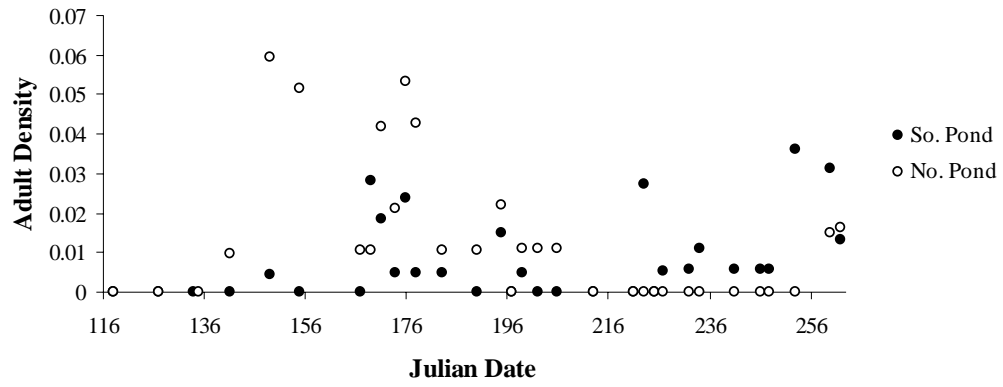


Figure 8: Comparisons of the average adult (A), metamorph (B), and larval (C) *R. draytonii* densities recorded during day and night surveys during the 2008 survey period in the northern pond (no *M. salmoides* present) and southern pond (9 juvenile *M. salmoides* present). Error bars represent the standard error.

A



B

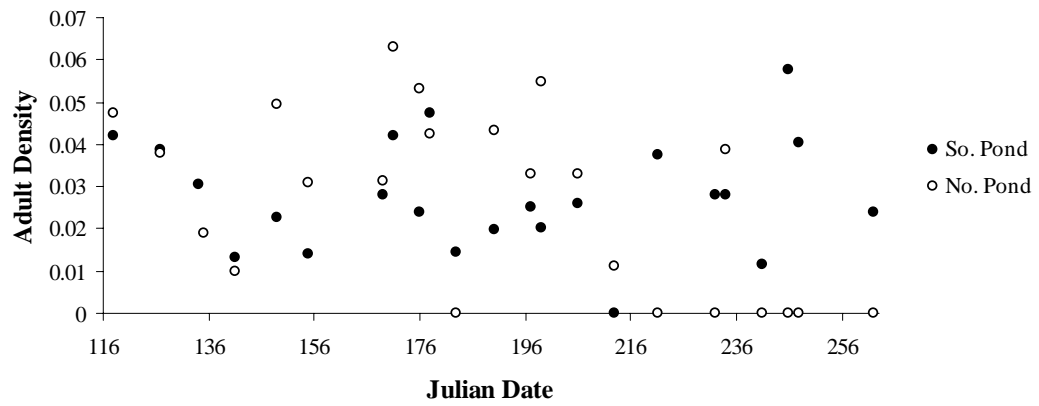


Figure 9. Densities of adult *R. draytonii* in the northern pond (*M. salmoides* absent) and southern pond (10 juvenile *M. salmoides* present) during the 2008 survey period.

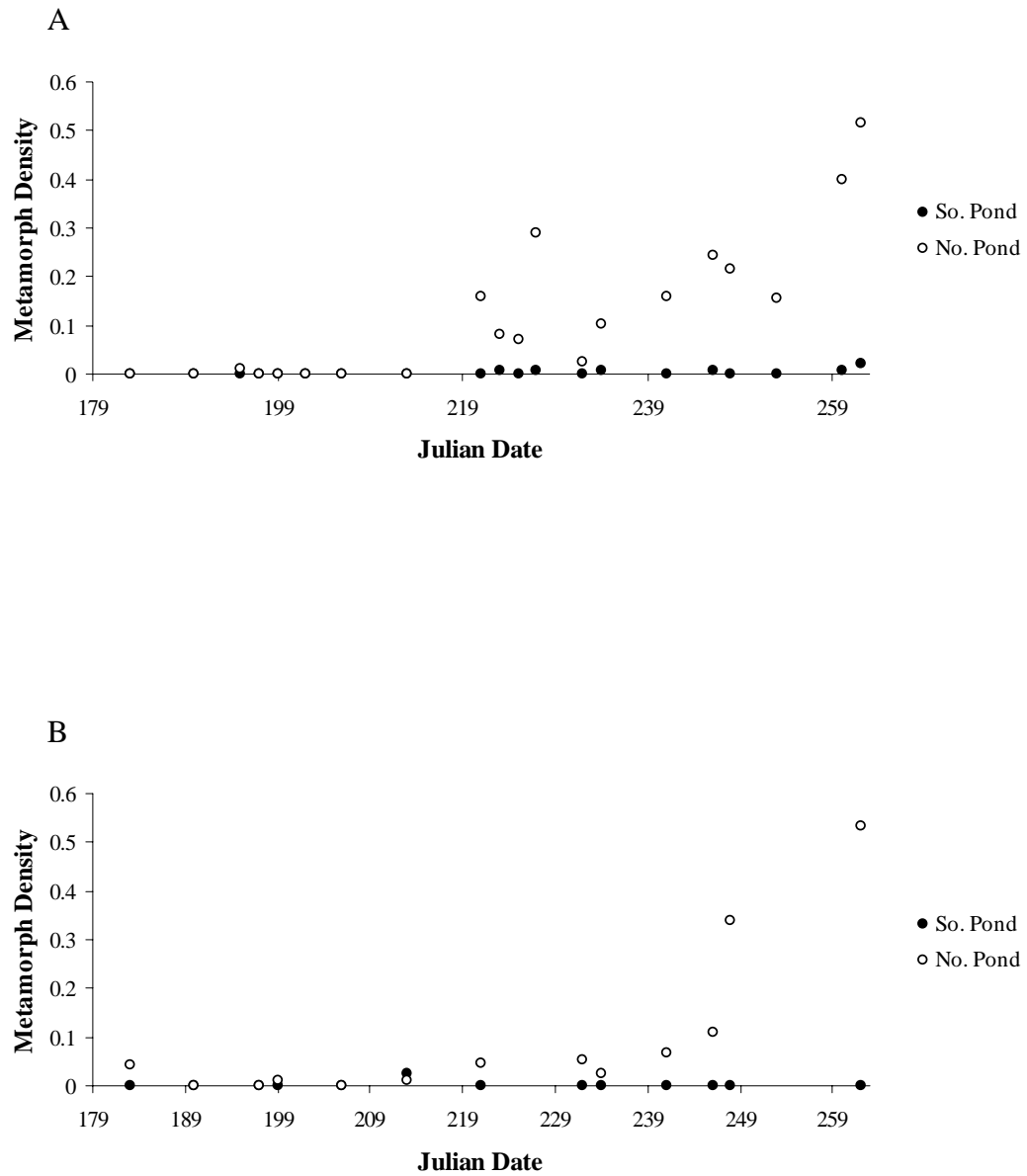


Figure 10. Densities of metamorph *R. draytonii* in the northern pond (*M. salmoides* absent) and southern pond (10 juvenile *M. salmoides* present) during the 2008 survey period.

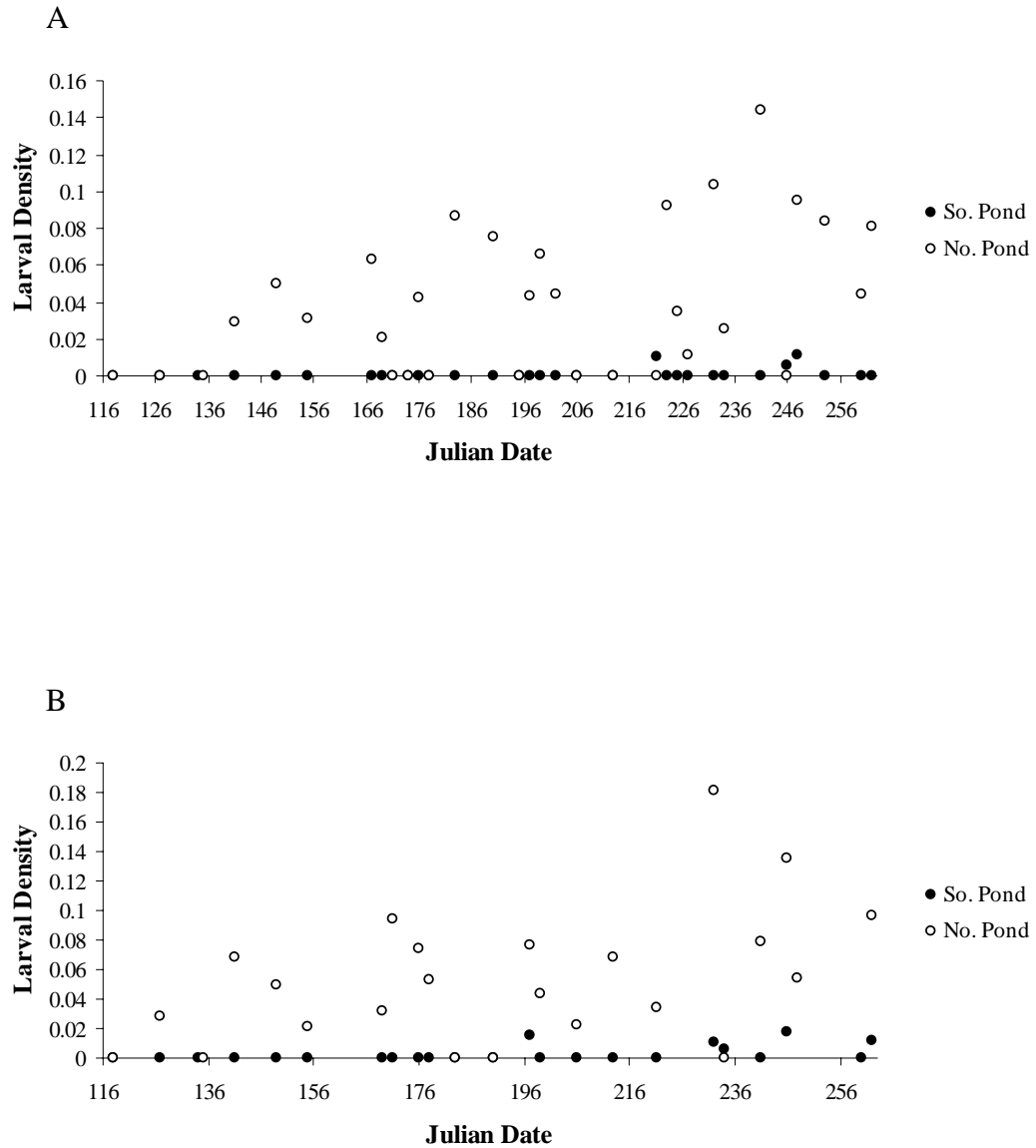
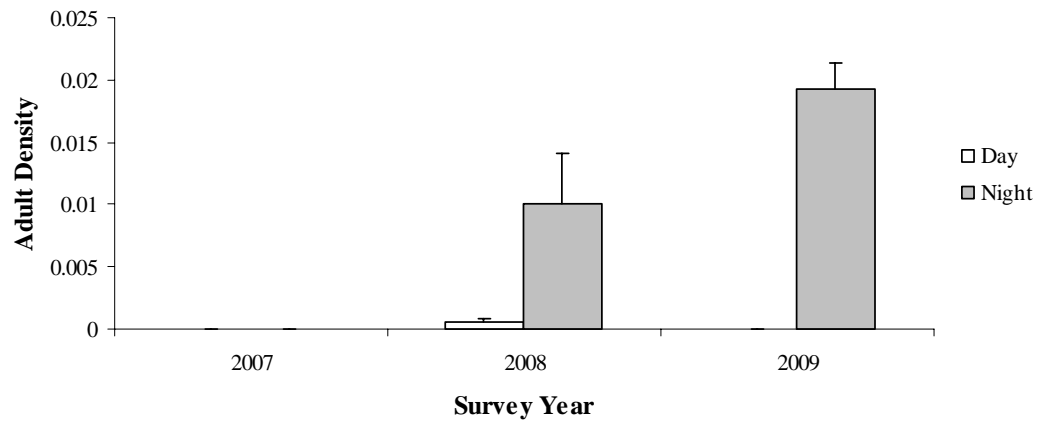
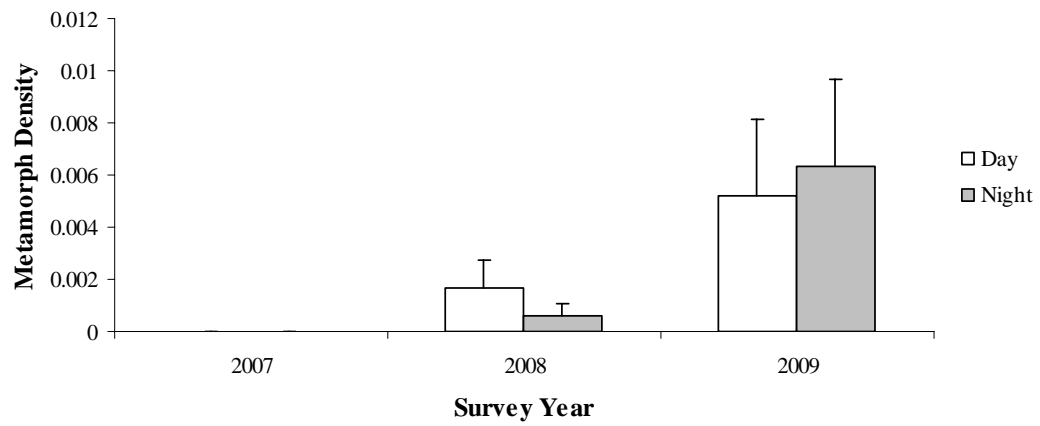


Figure 11. Densities of larval *R. draytonii* in the northern pond (*M. salmoides* absent) and southern pond (10 juvenile *M. salmoides* present) during the 2008 survey period.

A



B



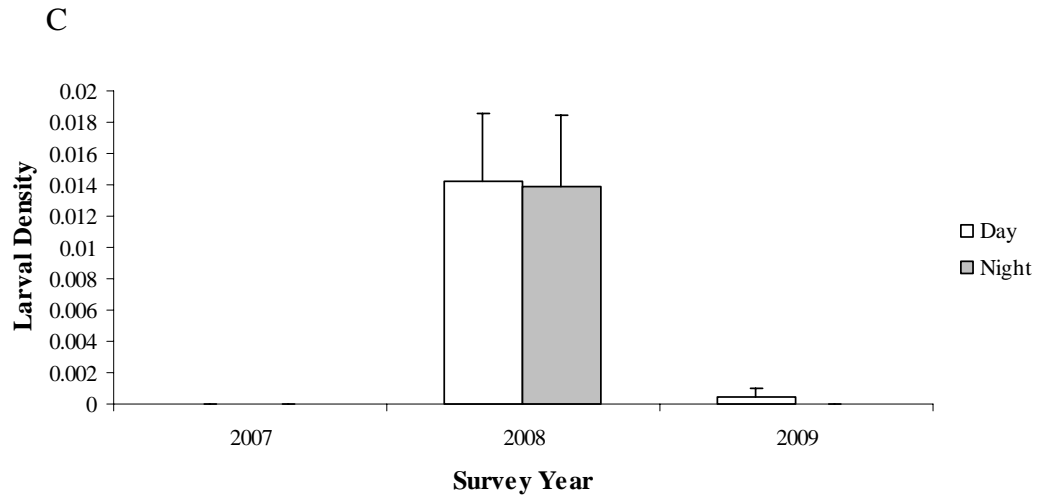


Figure 12: Comparisons of the average adult (A), metamorph (B), and larval (C) *P. regilla* densities in the southern pond recorded during day and night surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods. Error bars represent the standard error.

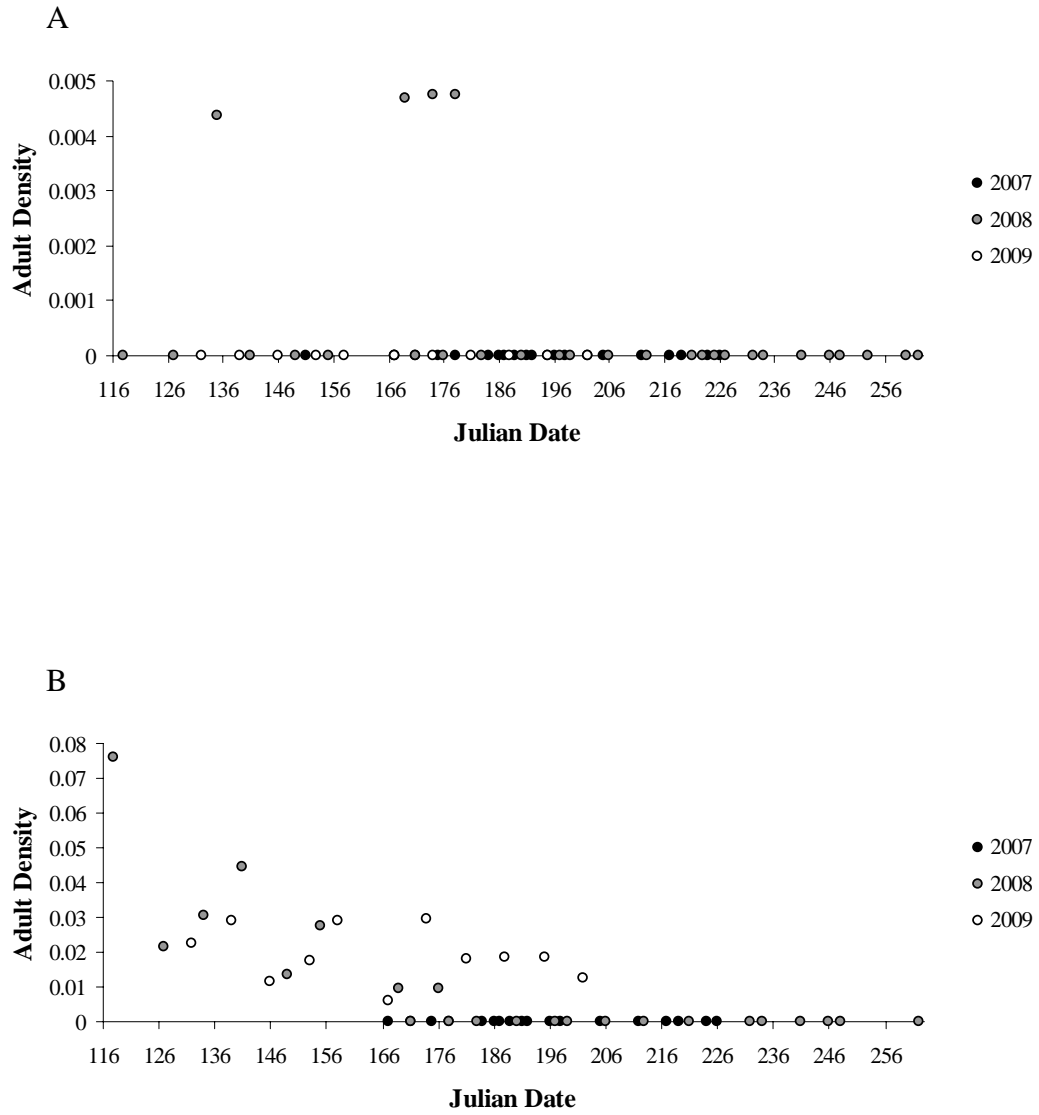


Figure 13. Densities of adult *P. regilla* in the southern pond recorded during day (A) and night (B) surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods.

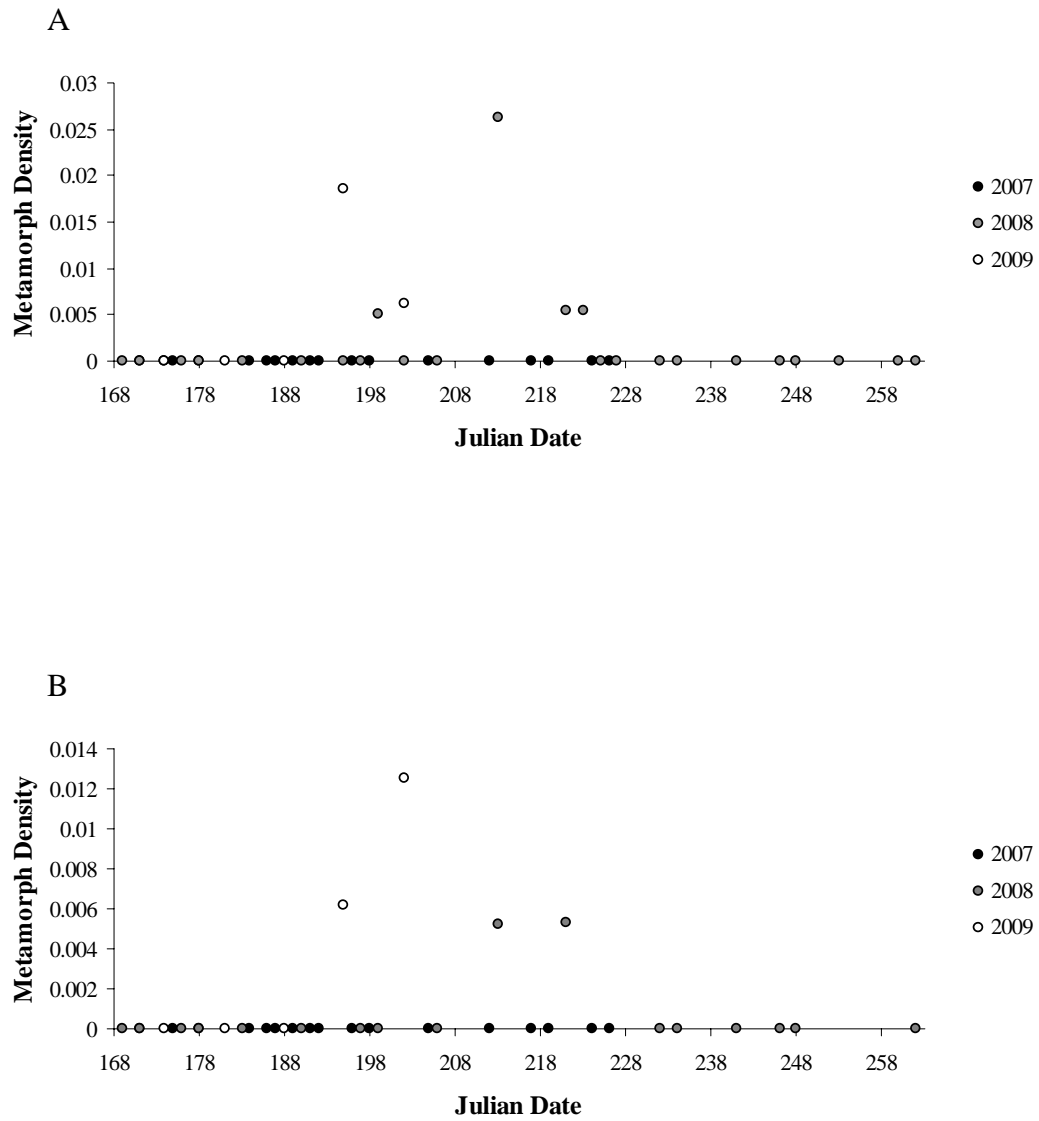


Figure 14. Densities of metamorph *P. regilla* in the southern pond recorded during day (A) and night (B) surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods.

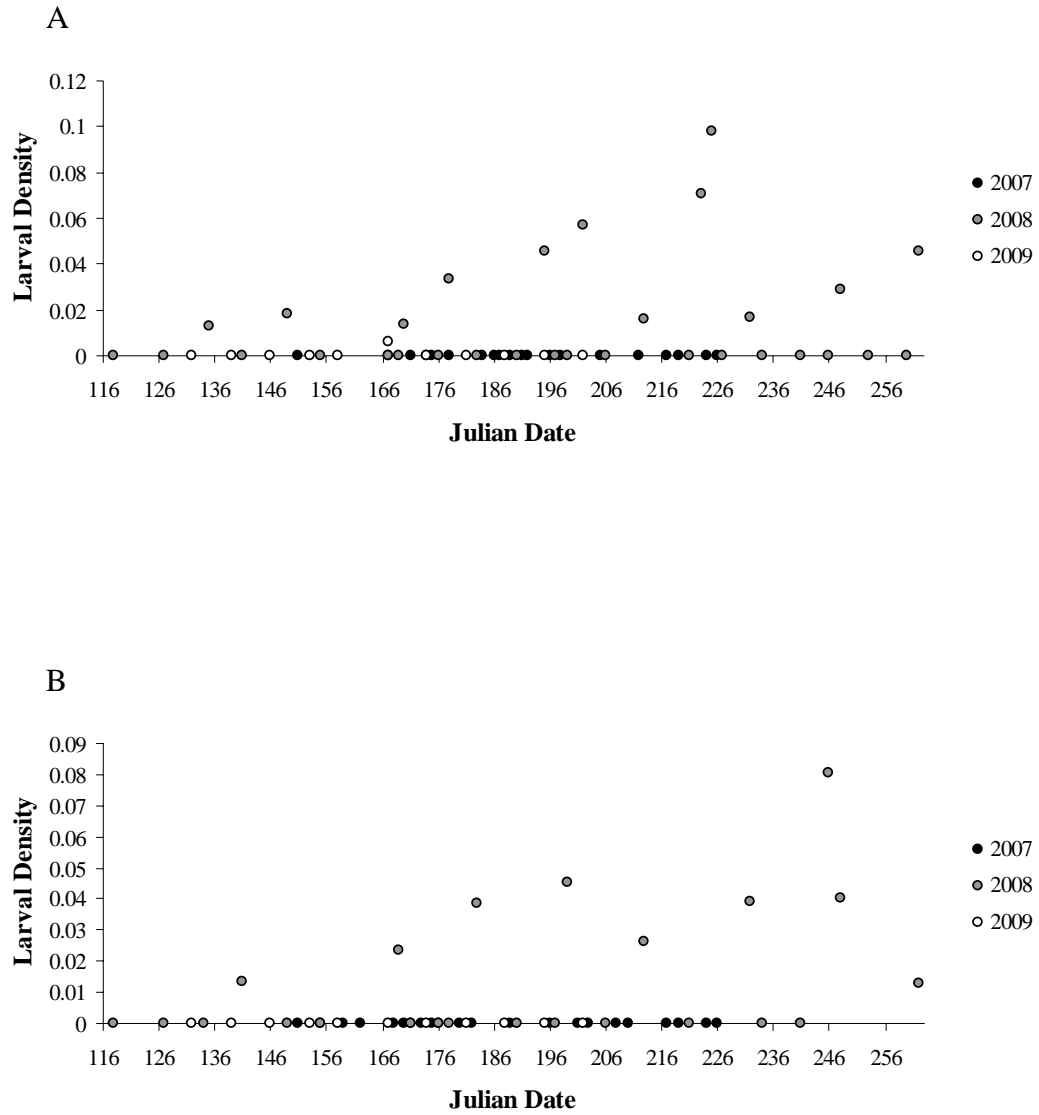
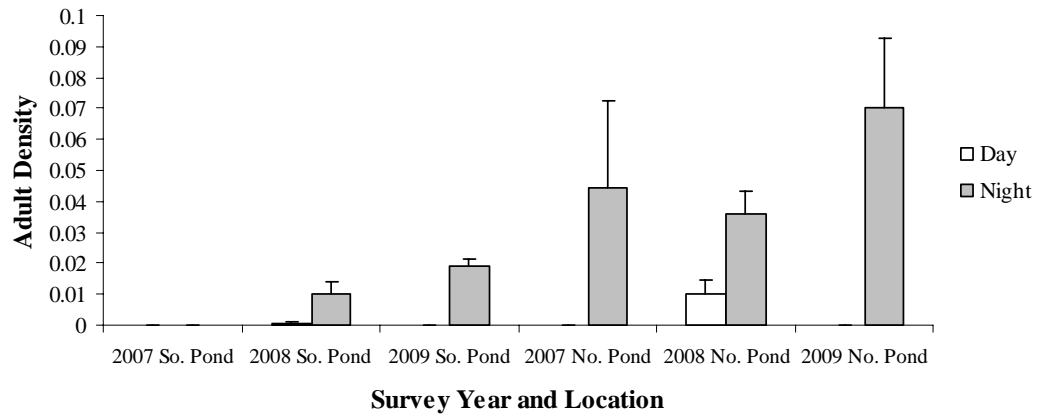
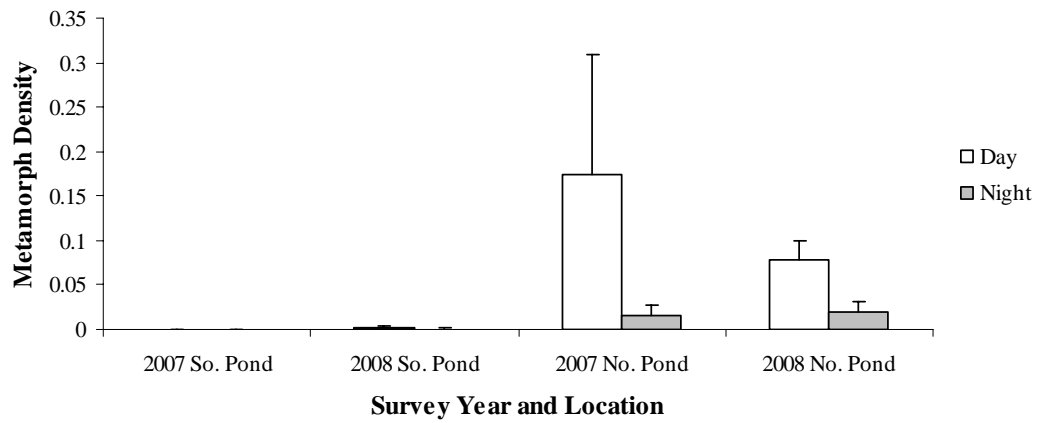


Figure 15. Densities of larval *P. regilla* in the southern pond recorded during day (A) and night (B) surveys during the 2007 (<3,000 *M. salmoides* present), 2008 (10 juvenile *M. salmoides* present), and 2009 (1 juvenile *M. salmoides* present) survey periods.

A



B



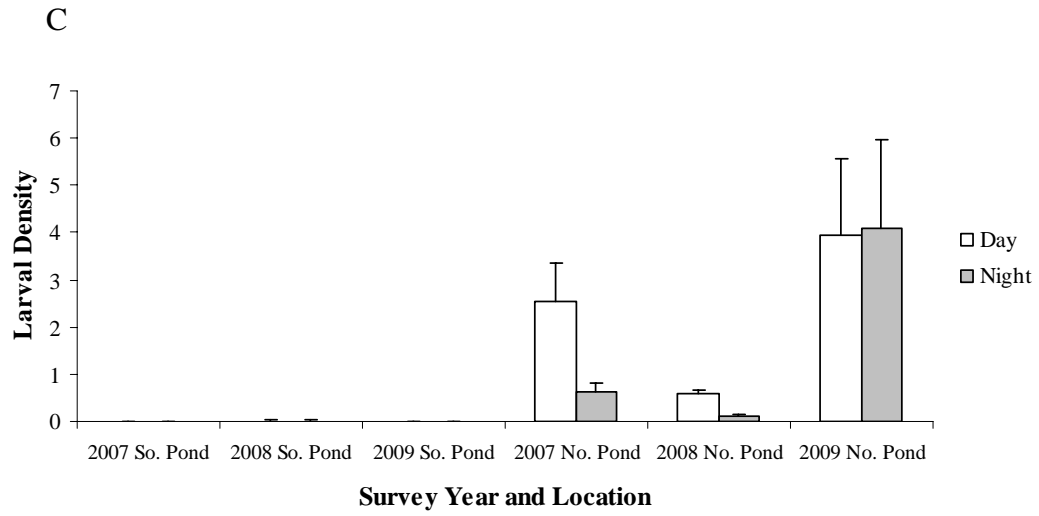


Figure 16: Comparisons of the average adult (A), metamorph (B), and larval (C) *P. regilla* densities in the southern pond and northern pond recorded during day and night surveys for all survey years. Error bars represent the standard error.

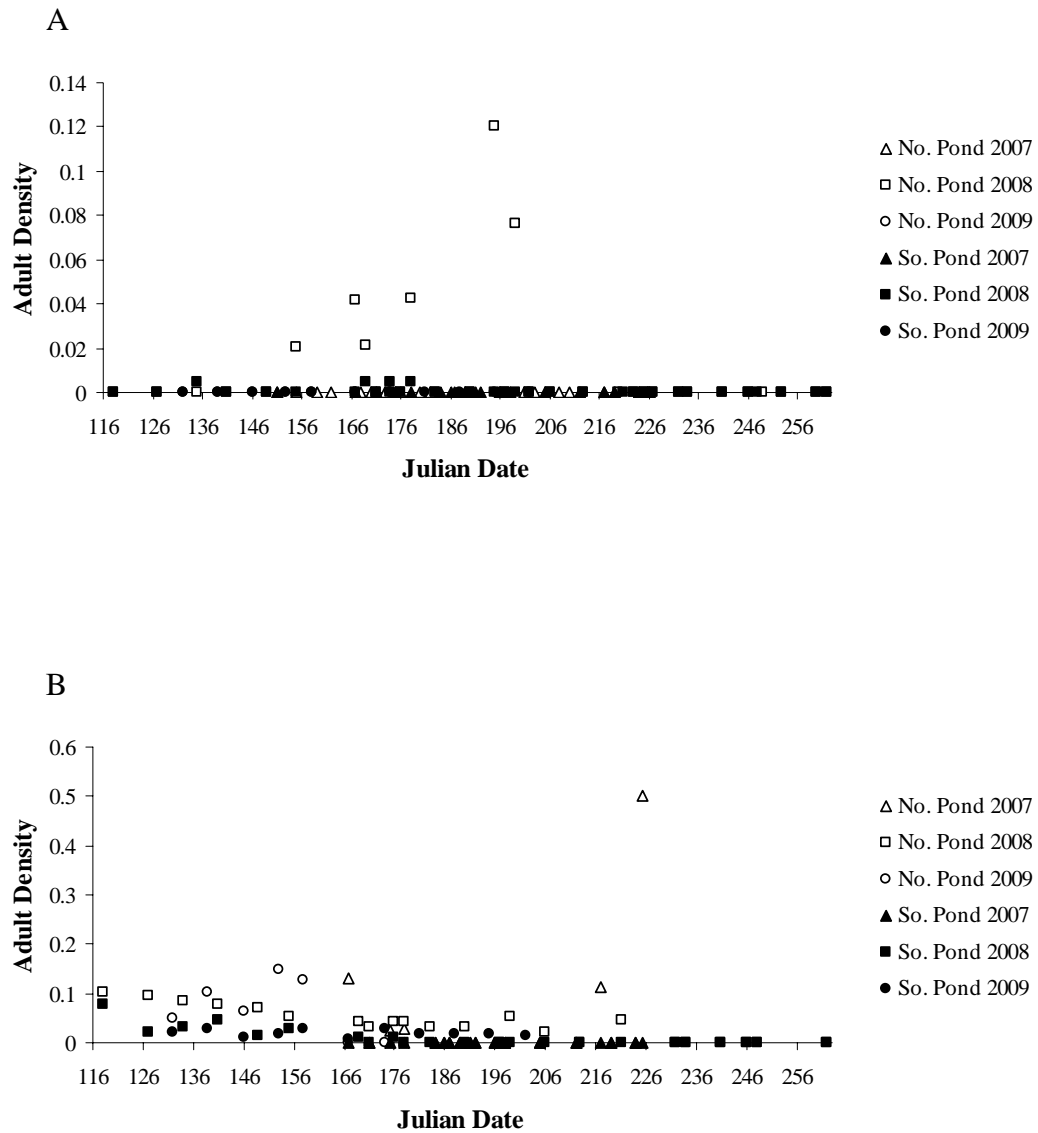


Figure 17. Densities of adult *P. regilla* in the northern pond and southern pond recorded during day (A) and night (B) surveys during the 2007, 2008, and 2009 survey periods.

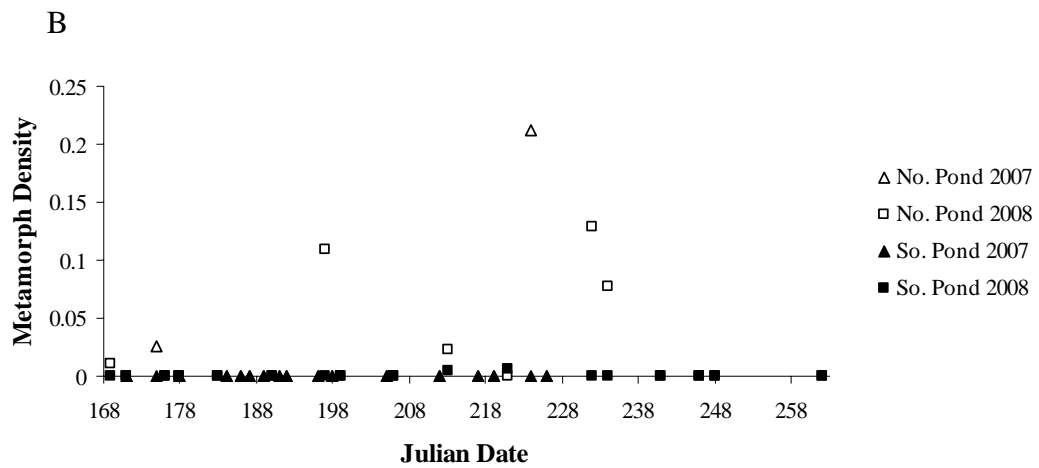
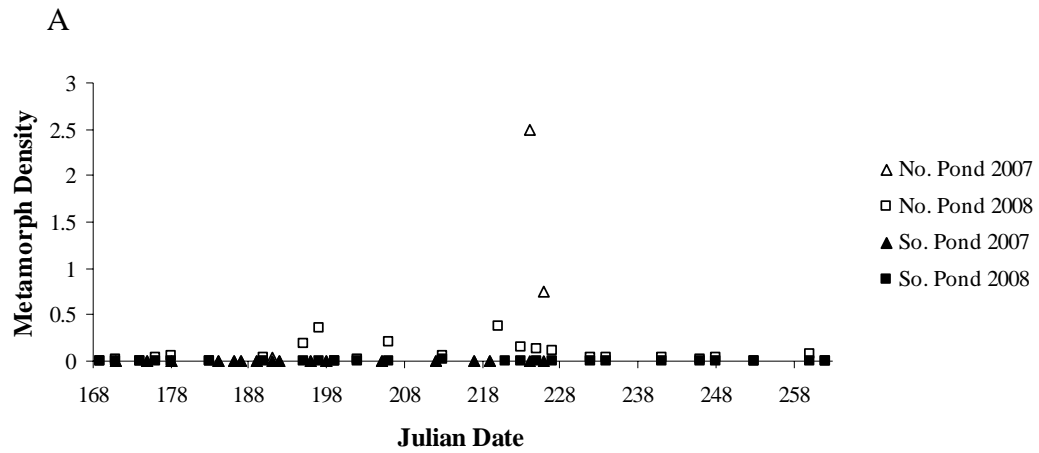


Figure 18. Densities of metamorph *P. regilla* in the northern pond and southern pond recorded during day (A) and night (B) surveys during the 2007, 2008, and 2009 survey periods.

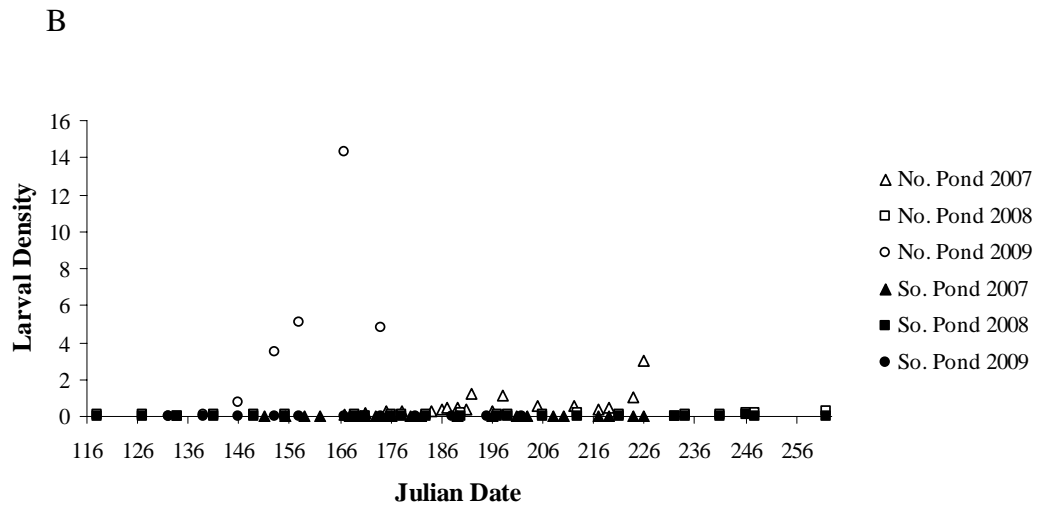
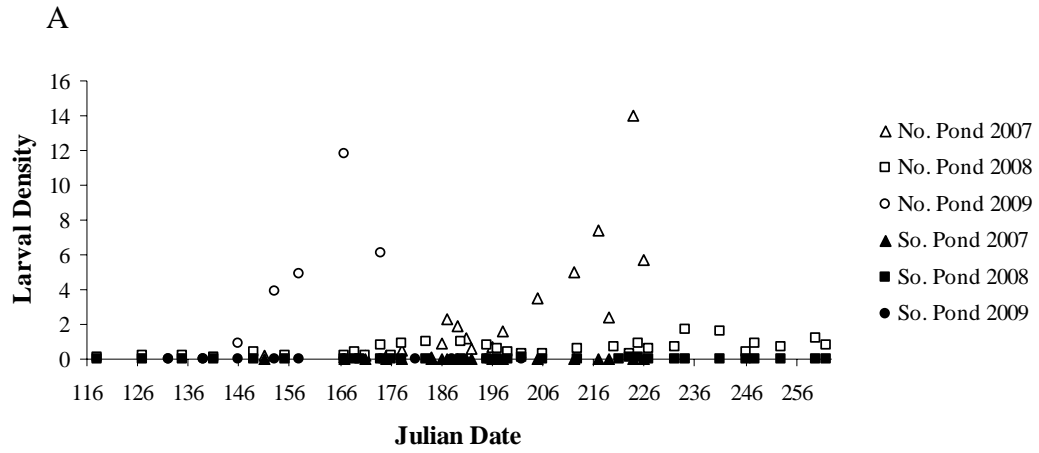


Figure 19. Densities of larval *P. regilla* in the northern pond and southern pond recorded during day (A) and night (B) surveys during the 2007, 2008, and 2009 survey periods.

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REGULATORY AGENCY AUTHORIZATION

Micropterus salmoides control was authorized by U.S. Fish and Wildlife Service Biological Opinions (file numbers: 1-8-03-F4 and 1-8-09-F/C-37), Army Corps of Engineers Section 404 of the Clean Water Act Certifications (file numbers: 200200768-JEM and 200200768-JWM), and a California Department of Fish and Game Streambed Alteration Agreement (file number: R5-2002-0129). Any additional authorizations to perform *M. salmoides* control extraneous to the conditions of the aforementioned documents were granted through personal communications between representatives of the applicable regulatory agency, Kenneth L. Gilliland, and Ms. Joddi Leipner of the Santa Barbara County Resource Recovery and Waste Management Division. All applied research was conducted under Kenneth L. Gilliland's California Department of Fish and Game Scientific Collecting Permit (SC-009081).